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CONTENTS

SOCIAL BEHAVIOR, REPRODUCTION, AND POPULATION CHANGES IN THE HOUSE MOUSE (*Mus musculus* L.)[1]

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INTRODUCTION

The present study of the interrelations of social behavior, reproduction, and population changes in the house mouse (*Mus musculus* L.) was undertaken in an effort to understand some of the aspects of natural population control in this species. This ubiquitous species apparently originated in grain-producing agricultural areas of central Asia (Dykstra 1950) and has long been associated more or less intimately with human habitation. The history of the house mouse is punctuated with numerous accounts of serious mouse population plagues, several of which have occurred within the past half century (Elton 1942). Hall (1927) reports a house mouse plague in Kern County, California in 1926 and 1927 and estimates the density of population in the center of the plague area at almost 70,000 house mice to an acre! There is little question of the economic importance of the house mouse, and it is considered a serious pest in many parts of the world. This economic importance lends considerable value to knowledge of the natural population control in this species.

The development of the Verhulst-Pearl-Reed logistic curve as a description of the growth form of human populations and of populations of laboratory animals (Pearl & Reed 1920; Pearl 1925) and the later applications of this curve to such divergent

forms as ants (Bitancourt 1941), sheep (Davidson 1938a, 1938b) and Norway rats (Emlen, Stokes, & Winsor 1948) indicate the importance of the sigmoid curve as a tool in the study of population phenomena. The upper limit or asymptote of the sigmoid curve of population growth is determined by the limitations of the environment of the species involved and is effected through the interactions of reproduction, mortality, emigration and immigration. The general shape of this curve of population growth indicates that these factors effecting natural population control begin to operate considerably below the upper asymptote and intensify as this limit is approached.

The factors involved in natural population control may be divided into those that are *density-independent* and those that are *density-dependent* (Smith 1935). The former operate on a constant percentage of the population independently of population density while the latter operate on a percentage of the population that changes as population density changes. The chief agents of population control appear to be density-dependent (Solomon 1949).

One of the more important ways in which density-dependent factors operate in controlling the upper asymptote of a population is through interspecific and intraspecific competition. Intraspecific competition, of primary concern in the present study, may depend on the establishment of certain special behavior patterns for its manifestation. The behavior patterns of interest here involve competition for area and for social dominance.

Intraspecific competition for area is characteristic of many vertebrates, among them sunfish (Greenberg 1947), lizards (Evans 1936), a large number of birds (Allee, et al. 1949; Howard 1948), eared seals (Brown 1947), howling monkeys (Carpenter 1934) and wood mice (Burt 1940). In these species the competition for area is characterized by a definite defense of breeding, feeding or nesting areas.

Competition for social dominance among vertebrates most frequently takes the form of establishment of dominance-subordination hierarchies. Various aspects of this social hierarchy have been worked out for a variety of domestic and laboratory animals, especially the domestic chicken and laboratory strains of the house mouse (Allee 1938, 1942; Collias 1944). In chickens social hierarchy usually takes the form of a straight-line peck right relationship among the individuals involved with the complete dominant able to peck all others without being pecked in return and the complete subordinate pecked by all others but unable to peck in return. Social hierarchy among laboratory mice is much more generalized and commonly involves a single dominant and partial or complete subordination among the other individuals in the group. Dominance-subordination hierarchies have been established for a number of other animals including the green sunfish (Greenberg 1947), geese (Jenkins 1944), quail (Emlen & Lorenz 1940), gibbons and rhesus monkeys (Carpenter 1940, 1942) and Norway rats (Calhoun 1950).

Although extensive work has been carried out on laboratory strains of the house mouse, especially on the physiological, reproductive, genetic, and behavioral aspects of its biology, until recently little attention has been focused on characteristics of the wild stock. Of late, however, accompanying the increase in interest in natural population phenomena, considerable attention has been directed toward the wild house mouse. This has resulted in such valuable studies as those in England by the Bureau of Animal Population, Oxford University (Elton 1942, Laurie 1946, Southern 1945, Southern & Laurie 1946), in North America by Evans (1949) and Young, Strecker, & Emlen (1950), and on Guam by Baker (1946). These studies have been primarily concerned with the measurement of various aspects of free-living, wild populations and will be referred to later in connection with the pertinent aspects of the present study. The status of present knowledge of competition for area and for social dominance in the house mouse will be discussed in Section II in conjunction with the experimental results from this investigation.

This investigation was divided into two major phases, each designed to supplement and provide information pertinent to the other. The initial phase of the investigation was on a free-living, wild population of house mice in a large barn on a Maryland farm. It was undertaken to provide a background for experimental work on the relation of reproduction in house mice to social organization. Of primary interest was the determination of population fluctua-tions, distribution of age groups and sex ratios, mortality, home range and seasonal movements, and the daily activity pattern. The second phase involved the establishment of a laboratory colony of house mice derived from wild stock from the farm, animal rooms at the University, and a local grain warehouse. Descendents of this stock were then used to study the interrelationships of reproduction, social organization and population levels.

It was hoped that by becoming familiar with a wild population the problems involving social organization would be better understood and possibly more easily solved. One of the problems in the study of social phenomena is that of understanding them as they operate in their proper context, the wild population where they originally evolved. Since the aim was to ultimately bring the populations into the laboratory and thus facilitate better observation and more exact measurement of social phenomena it was felt that the first practical move was to acquire some understanding of the action and results of these social phenomena in their natural setting, the wild population. It was also hoped that this knowledge would aid in the recognition of possible new and aberrant behavior imposed by the new environment. It was believed that these laboratory investigations might in turn shed light on the mechanism of some of the events occurring in the wild population under study and to give a more complete picture of some of its actions and characteristics. By keeping in close touch with both the field and the laboratory, the transfer of knowledge gained in one to the other would be easier and less subject to speculative error.

I. HOUSE MOUSE POPULATION CHANGES ON A MARYLAND FARM

House mice appear to be extremely adaptable and are found in a great many diverse habitats ranging from cold storage warehouses (Laurie 1946) to open fields (Linduska 1950). One of the more commonly occupied habitats is farm buildings. Analyses of the reproductive aspects of farm mice were made by Laurie (1946) and Southern & Laurie (1946) who studied mice living in grain ricks in England. Little has been done, however, on other aspects of farm mouse populations. Of these aspects, those dealing with population fluctuations, age groups, sex ratios, mortality, movements and daily activity will be considered here.

METHODS

The field work was carried out on a farm near Baltimore, Maryland, and extended from November 1948 to October 1950. The chief activity on the farm was breeding and boarding race horses, and the stock consisted of fifty to sixty horses, ten to twelve cows, 100 chickens and ducks, two or three pigs, three or four dogs and an occasional stray cat. The four main farm buildings were built largely of wood and consisted of two horse barns, an empty corn crib with attached tool shed and horse stalls, and a large hay barn with facilities for a number of horses and cows. All of the buildings were in need of repair.

The mouse population studies were largely confined to the hay barn. This building was 121 feet long and 64 feet wide with a central hay mow on the main floor which extended upward and occupied all of the second floor of the barn. Peripheral to the hay mow on the main floor were horse stalls and three rooms for other livestock. During the winter the calf room and the cow room contained calves, cows, and pigs; the third room was used for hay storage. The clay floor of the hay mow and horse stalls was covered with straw, and the three rooms had concrete floors. A large door gave access to the hay mow in the center of each of the long sides of the barn, and in the winter the north door was walled up with bales of hay tightly packed and several rows deep. Feed for the horses and cows was kept in wooden bins and placed in feeding troughs once or twice a day. Water was available in pails in each stall, and a leaky automatic water system was in use in the calf room and cow room. Most of the hay and straw used was stored in bales in the central part of the hay mow; and during the fall, winter, and early spring the supply was renewed almost weekly from local dealers.

The hay barn was bordered on two sides by a field of short grass, on one side by a small plot containing old pieces of farm equipment and dense, short weeds, and on the fourth side by farmyard and buildings. A road formed the far border of the small plot.

Live-traps were used exclusively and were of two types, the small-sized metal Sherman trap and a trap made from a quart metal can and a museum special trap. The traps were scattered fairly evenly throughout the building and around the outside placed according to the signs of mouse activity. Because of the constant removal and addition of new hay in the center of the hay mow it was impossible to trap that area thoroughly. The traps were baited with peanut butter, and in cold weather a handful of hay and some cracked corn were added to minimize mortality. The number of traps used varied with the amount of fresh mouse signs but was never more than 100 or less than 60. Traps were examined around 9:00 a. m. and 4:30 p. m. Trapping periods varied from one to five days but were usually either one or two days in duration. Trapping was conducted on a total of 43 days.

Captured mice were sexed, weighed on a portable scale accurate to about one gram, and the location was recorded. In addition, the condition of the vaginal orifice and size of mammae of females were noted and an estimation of whether or not they were pregnant was made. The mice were then individually marked by toe-clipping and released at the point of capture. Capture locations were recorded on accurate, detailed maps of the various sections of the barn. Since the mice used the walls as well as the floors, maps of the walls were added to each side of the map. Information on changes in farm practice, disposition of livestock, location of feed bins, and other similar data were added to the set of maps used for each trapping period.

The population levels of mice in the barn are stated in terms of mice caught per 100 trap-hours, referred to hereafter as trap success. Some traps were accidentally sprung, and it was assumed that these traps were sprung at an arithmetic rate. Thus the average number of hours that these traps were available for catching mice was 50 per cent of that for unsprung traps. Therefore, the number of traps accidentally sprung was divided by two and subtracted from the total number of traps used during the period. For example, if 100 traps were set in the afternoon and when run the next morning six were found accidentally sprung, one-half of this number was subtracted from the total, leaving 97 traps as the adjusted numbers of traps assumed to be in operation for the period. The number accidentally sprung rarely exceeded five per cent of the total set and was usually considerably below this. Trap hours were figured to the nearest half hour from the midpoint of the time spent running the traps. Trap hours were used because the traps were run twice a day and the time of running varied enough to make estimation of trap success based on a twenty-four hour period not feasible. The use of trap-hours also facilitates comparison of diurnal and nocturnal trap success and gives it a more accurate basis.

The activities of house mice and the method of trapping do not produce anything closely approaching a random sample and therefore a simple trap success index for the population levels was used. Estimates by more direct methods, such as the Lincoln Index or similar ratio methods (Jackson 1939), are unsatisfactory; first, because the length of time between trapping periods was so long in some cases that significant population changes had occurred and, second, because of the non-random sampling. It is believed that the trap success index used gives a reasonable indication of the magnitude and direction of the population changes.

Hythergraphs showing the weekly mean temperatures and total weekly precipitation for the duration of the study were used to establish biologically useful seasons, (Figures 1 and 2, Table 1). Each of these seasons shows relatively homogeneous temperature and rainfall conditions. There are typically seven seasons in a year. This method uses a base that appears biologically more sound than that of calendar seasons (Davis & Hall 1948).

HYTHERGRAPH BY WEEKS - BALTIMORE, MD.
JANUARY 1, 1949 TO DECEMBER 31, 1949

HYTHERGRAPH BY WEEKS - BALTIMORE, MD.
JANUARY 1, 1950 TO DECEMBER 31, 1950
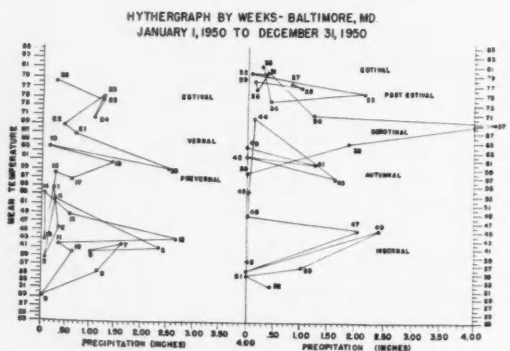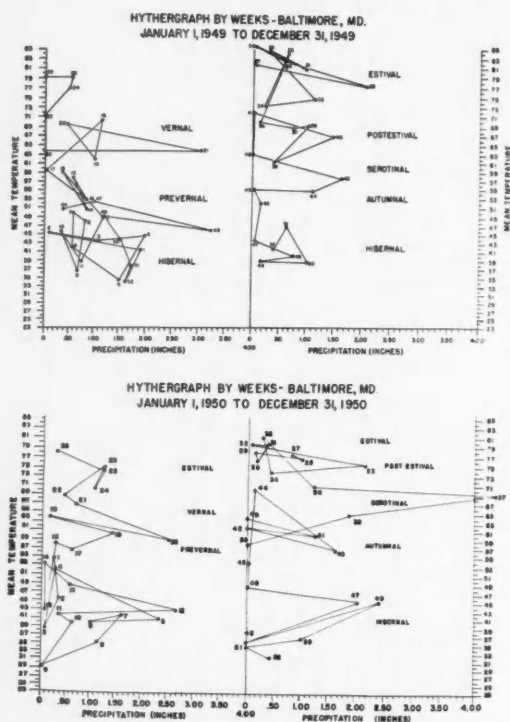
TABLE 1. Biological seasons as determined from hythergraphs (Figs. 1 and 2).

Season	Dates
Hibernal	Dec. 17, 1948 - Mar. 24, 1949; Nov. 18, 1949 - Apr. 14, 1950
Prevernal	Mar. 25 - Apr. 28, 1949; Apr. 15 - May 19, 1950
Vernal	Apr. 29 - June 9, 1949; May 20 - June 16, 1950
Estival	June 10 - Sept. 1, 1949; June 17 - Aug. 12, 1950
Postestival	Sept. 2 - Oct. 13, 1949; Aug. 13 - Sept. 9, 1950
Serotinal	Oct. 14 - 27, 1949; Sept. 10 - 23, 1950
Autumnal	Nov. 11 - Dec. 16, 1948; Oct. 28 - Nov. 17, 1949; Sept. 24 - Nov. 11, 1950

RESULTS

The results that follow are largely derived from the trapping procedures just outlined. The population fluctuations are stated in terms of trap success, an index relying chiefly on the similarity of these trapping procedures throughout the study. The weight and age distribution was determined from the weights and examination of the reproductive condition of the mice. Analysis of the data on recaptured individuals gave estimates of home range. Sex ratios were also determined. The seasonal distribution of mice in the barn was established from the detailed maps made for each trapping period. Diurnal and nocturnal trapping results gave insight into the daily activity rhythm. The data on recaptured individuals also gave information on the presumed disappearance of marked individuals from the population. Interspecific relations among the mice and other animals

in the barn were determined by direct observation and from studies that were being conducted on these animals concurrently with the house mouse studies. *Trap Success.* The seasonal trap success for the mouse population in the hay barn is presented in Table 2 with a statistical analysis of the variance.

TABLE 2a. Seasonal trap success.

Season	Number of trap periods	Total captures	Trap hours	Captures per 100 trap hours
Autumnal, 1948	1	108	9578.5	1.13
Hibernal	4	64	11889.0	0.54
Prevernal, 1949	2	41	4033.0	1.02
Vernal	3	31	5700.0	0.54
Estival	2	9	7187.5	0.13
Postestival	1	17	3179.0	0.54
Serotinal	1	76	7077.0	1.07
Autumnal	1	57	2981.5	1.91
Hibernal	5	61	9396.5	0.65
Prevernal, 1950	2	42	3696.5	1.14
Vernal	1	15	1807.5	0.83
Estival	1	12	1934.5	0.62
Postestival	1	11	1728.0	0.64
Serotinal	1	13	1788.5	0.73
Autumnal	1	19	1915.5	0.99

TABLE 2b. Analysis of variation.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F value	5% level
Seasons	6	1.5801	.2634	2.39	4.28
Years	1	.0016	.0016	0.01	5.99
Error	6	.6598	.1100		
Total	13	2.2415			

As can be seen in Table 2b, this analysis of variance does not show any statistically significant differences between either the seasons or the years. There is a rather large experimental error in the attempts to measure this mouse population and this implies therefore that the simple analysis of variance test in Table 2b would have low sensitivity. This means that a large number of the seasonal effects would produce differences of the same order of magnitude as the experimental error. Hence, the small seasonal effects could not be detected by an analysis of variance.

Dr. Irwin D. J. Bross of The Johns Hopkins University furnished a more sensitive test and because of its importance to the material presented and also its possible application by other workers, his explanation of this test is presented here.

"In an effort to improve the sensitivity, the statistical technique of 'individual degrees of freedom', a device which allows the various seasonal effects to be studied *separately*, was employed. According to *previous* biological experience, the hibernal and estival seasons represent population troughs, whereas peaks occur in the prevernal and autumnal seasons. The main seasonal effect would be the difference be-

tween trough and peak seasons. Biological experience also indicates other seasonal effects, such as a difference between the heights of the prevernal and autumnal peaks, but these effects would be expected to be of a much smaller magnitude.

"The general 'seasonal effect' of Table 2b was therefore analysed into six separate seasonal effects. When the separation was made, the difference between peak and trough seasons turned out to be an effect that was significant at the 5% level (11.06). The five other seasonal effects turned out to be nonsignificant and have therefore been recombined in Table 2c under the heading 'Other seasonal effects'."

TABLE 2c. Analysis of seasonal effects.

Source of variation	Degrees of freedom	Sum of squares	Mean square	F value	5% level
Biological peaks vs. troughs.....	1	1.2168	1.2168	11.06	5.99
Other seasonal effects.........	5	.3633	.0727	.66	4.39
Error............	6	1.5801	.2634		

Examination of the graph of seasonal changes (Fig. 3) reveals considerable similarity between the two years of observations both in the time and magnitude of these changes. For example, the trap success for the two hibernal seasons is 0.54 and 0.65 respectively, and for the two postestival seasons is 0.54 and 0.64 (Table 2a). In addition, observations of the changes of signs of mice in the barn (fresh droppings, runways, and sight records) not only correlate very well with the changes in abundance suggested by the graph but indicate a further repetition of this pattern of peak and trough populations extending into early 1951 after all trapping had ceased. Mouse signs, especially sight records, increased markedly in the late autumnal season of 1950, dropped off during the hibernal season and increased again in the prevernal season of 1951. Biologically, the most important aspects of population fluctuation in the barn are the peak populations in the prevernal and autumnal seasons, the trough populations in the hibernal and estival seasons, the similarity in time and magnitude of these seasonal changes, and the difference between the estival seasons of the two years (0.13 and 0.62). The relationships between these aspects and other characteristics of the mouse population will be discussed later.

Weight and Age Distribution. The distribution of weights of captured house mice (Table 3) indicates, by the low numbers of small mice captured, the selective nature of the trapping procedure. On the basis of normal population age distribution and mortality one ought to expect much higher numbers of younger and smaller mice. Laurie (1946) found a similar weight distribution when using kill-trapping methods on house mice in natural environments, but when something approximating the total population was captured by other methods a much higher proportion

of young was recorded. The distribution recorded here is a reflection of the trappable portion of the population and is affected by the size of the home range of the mice.

TRAP SUCCESS (mice/100 trap hours)
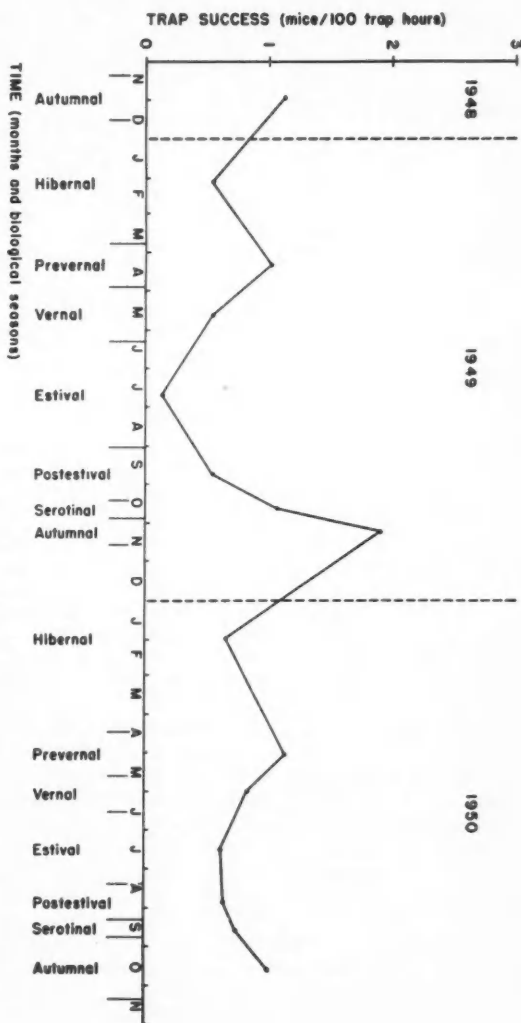
The rapid decline in the percentage of males beyond the 16 gram class probably reflects the fact that heavy pregnant females shift the weights for that group in an upward direction.

Two age classes for the population were established on the basis of weight and reproductive condition. Table 3 shows that in the twelve gram class approximately 50% of the females captured had perforate vaginal orifices and this weight class is used as the separation between the two classes. There was no evidence of secondary closure of the vaginal orifice after initial perforation. All mice in the twelve gram class and below are called *immature*, all above this

TABLE 3. Weight distribution of house mice.

Midpoint weight classes (Grams)	FEMALES			Total Animals	Percent Males
	Total	Percent with perforate vaginal orifice	Males		
4........	1	0.0	1	2	50.0
6........	1	0.0	0	1	0.0
8........	5	0.0	4	9	44.4
10........	13	38.5	21	34	61.8
12........	56	48.2	50	106	47.2
14........	39	76.9	77	116	66.4
16........	38	92.1	95	133	73.2
18........	33	100.0	65	98	66.3
20........	17	100.0	11	28	39.3
22........	6	100.0	3	9	33.3
24........	3	100.0	0	3	0.0
26........	2	100.0	0	2	0.0
28........	1	100.0	0	1	0.0
Total...	215		327	542	60.3 unweighted percentage 37.1 weighted percentage*

*Calculated on the basis of 100 individuals in each weight class.

class are called *mature*. Although the perforation of the vaginal orifice is not a highly accurate criterion of sexual maturity in the house mouse (Laurie 1946), it was the only criterion available for a study in which the mice were immediately released alive in an effort to reduce the amount of handling to as short a time as possible. Laurie found that in house mice living wild in England sexual maturity was attained in females at a slightly lighter weight than in males. Snell (1941) states that "maturity in males occurs at about the same time as in females or perhaps somewhat later."

In an effort to determine the relationship between reproductive rates, survival of young, and the population changes suggested by Figure 3, an analysis was done of the number of immatures and the different population phases (Tables 4 and 5). A chi-square test (Fisher 1936) on the number of immatures captured during different population phases (Table 5a) indicates a statistically significant difference among these phases. Chi-square tests were then run on comparisons of the number of immatures captured for each of the differences in population phase (Table 5b). Statistical significance exists between trough and peak, increasing and trough, and decreasing and trough populations. Biologically this suggests that there was either an increase in survival or in reproductive rate during the increasing phase of population change, for during this phase the per cent of immatures was highest. This high percentage carries over to the peak population and then drops off as the population begins to decline. When the population reaches the trough phase the percentage of immatures is lowest. There is no evidence from this study indicating whether it was differences in survival or in reproductive rate or a combination of both that was responsible for these changes in the number of immatures. The work of Parkes (1924) on laboratory mice indicates that in the colder seasons there may

TABLE 4. Seasonal age composition of house mouse population.

Season	Immature	Mature	Total	Percent Immature
Autumnal...	24	79	103	22.2
Hibernal....	11	53	64	17.2
Prevernal....	16	25	41	39.0
Vernal......	10	21	31	32.3
Estival......	2	7	9	22.2
Postestival..	5	12	17	29.4
Serotinal....	23	53	76	30.3
Autumnal...	20	37	57	35.1
Hibernal....	14	47	61	23.0
Prevernal....	8	34	42	19.0
Vernal......	5	10	15	33.3
Estival......	2	9	11	18.2
Postestival..	0	11	11	0.0
Serotinal....	4	9	13	30.8
Autumnal...	8	11	19	42.1
Total.....	152	418	570	26.7

TABLE 5a. The relationship of immature mice captured to population phases.

Population phase	Immatures captured	Total captured	Percent immatures
Peak............	44	140	31.4
Trough..........	29	156	18.6
Increasing.......	40	125	32.0
Decreasing.......	39	149	26.2
Total..........	152	570	

$X^2 = 8.60$	3 d.f.	$P < 0.05$

TABLE 5b. Chi-square tests for differences in population phases.

Comparison of phases	X^2 Value	Degrees of freedom	P Value
Peak and Trough.......	6.99	1	<0.01
Increasing and Trough..	8.15	1	<0.01
Decreasing and Trough..	5.64	1	<0.02
Increasing and Decreasing...........	1.61	1	>0.20

be a change in the reproductive rates. He found that when mice were kept at outside temperatures in England no litters were born from November to February but that at inside temperatures they bred all year. It is therefore possible that the drop in the percentage of immatures during the trough populations is due, in part at least, to change in the reproductive rate during the hibernal seasons.

An analysis of the relationship between the number of animals captured during a trapping period and the number of immatures captured shows no statistically significant difference (Table 6) and indeed, the similarity of the percentage of immatures in the different numbers of animals captured suggests that the samples were very homogeneous.

TABLE 6. The relationship between number of captures per trap period and the number of immature mice captured.

Number of captures per trap period	NUMBER OF CAPTURES		Percent immatures
	Immature	Total	
1-25............	26	95	27.4
26-50...........	34	114	29.8
51-75...........	45	182	24.7
76-100+........	47	179	26.3
Total.........	152	570	

$X^2 = 1.12$ 3 d.f. $P > 0.99$

Home Range and Movements. Data on home range of mice on the farm are derived from the recapture of 92 individual mice (59 males and 33 females) a total of 129 times. Of these, 75.0% were recaptured once, 18.6% twice, and 7.4% were recaptured three or more times.

The low number of multiple recaptures and the typical activity patterns of house mice do not make possible the description of their home range in areal terms. Rodents commonly dwelling in man-made structures typically follow routes and trails determined by the construction of the buildings and do not as a rule spread their activities over large areas (Davis, Emlen, & Stokes 1948; Young, Strecker, & Emlen 1950). House mice in the barn typically traveled horizontally and vertically along walls, and when foraging for food made short direct dashes to any food on the open floor from the nearest cover. Since description in areal terms also necessitates a minimum of three recaptures to produce other than long narrow ranges for animals known to move in many different directions a linear unit of measurement was adopted for description of the home range.

As Young, Strecker, & Emlen (1950) point out, in a large series there is little difference between home range determined by measurement of movements from point of initial capture or from points of subsequent recapture if there has been no distortion by individuals with unstable or progressively shifting home ranges. In small series such as this, where there is evidence of shifting home range, the measurements of movements from point of initial capture tend to be larger than from points of subsequent recapture. Also, initial captures on the periphery of the range of an animal produce distortion which is of considerable significance in small series. For these reasons the data on home range presented here are based on distances between points of subsequent recapture.

Mice in the barn were found to have a rather restricted home range. The arithmetic average distance traveled (Table 7) was 17.2 ft., and the longest move was 79 ft. This table also shows that 97.7% of all animals move no more than 50 feet and 79.1% moved up to 30 ft. These mice have a slightly larger home range than house mice living in animal buildings at the University of Wisconsin (Young, et al., 1950) where 90% of the movements were not more

TABLE 7. Home range measurements—distance between successive captures

	DISTANCE BETWEEN SUCCESSIVE CAPTURES (feet)							Total	Average distance traveled
	0-10	11-20	21-30	31-40	41-50	51-60	61-70		
Males...........	34	14	12	6	14	0	3	83	19.9
Females.........	23	14	5	3	1	0	0	46	12.4
Total.........	57	28	17	9	15	0	3	129	17.2
Percent of total males........	41.0	16.9	14.4	7.2	16.9	0.0	3.6		
Percent of total females.......	50.0	30.4	10.9	6.5	2.2	0.0	0.0		
Percent of total...	44.2	21.7	13.2	7.0	11.6	0.0	2.3		
Cumulative percentage									
Males...........	41.0	57.9	72.3	79.5	96.4	96.4	100.0		
Females.........	50.0	80.4	91.3	97.8	100.0	100.0	100.0		
Total...........	44.2	65.9	79.1	86.1	97.7	97.7	100.0		

than 30 ft. and 70% were not more than 10 ft. The longest move made by a male was 79 ft. from point of initial capture, and the longest move by a female was 45 ft. Females moved an average of 12.4 ft. and males moved an average of 19.9 ft.; 91.3% of the males move no more than 30 ft.

In order to determine if there had been any shifts in home range during the period of study an analysis of the distance moved from point of initial capture was made with reference to length of time from capture. Only a few observations were available on female movements. There was no evidence of a change in average distance moved over the period involved. During the first 20 days after the initial capture, eight recaptured females moved an average of 13.5 ft. Nineteen females recaptured between 21 and 40 days after initial capture had moved 11.1 ft. Three females recaptured between 101 and 120 days later had moved 15.3 ft. and three others recaptured 121-140 days later had moved 11.3 ft. Although the evidence is meager this suggests little or no shifting of home range. On the other hand males showed a marked increase, especially after 20 days. Twenty-eight males recaptured during the first 20 days after initial capture had moved an average of 10.1 ft. Eighteen recaptured between 21 and 40 days had moved 21.5 ft. The four males recaptured between 101 and 120 days after initial capture had moved an average of 13.3 ft. but all other captures up to 200 days after initial capture were above 24 ft. and most were above 35 ft. This strongly suggests a certain amount of shifting of ranges among the males.

A factor influencing home range of both sexes is that of density of food supply. The average distance moved within the hay mow was 25.7 ft. for males, 13.4 ft. for females. Average movements to and from the hay mow were 32.7 ft. for males and 16.8

ft. for females. Within the peripheral rooms males
and females moved an average of 9.7 and 9.5 ft.
respectively. In and around the hay the density of
food (seeds) per unit area is low when compared
with the rooms where the food is concentrated in bins
and feeding troughs. Correspondingly, the average
distances traveled between captures in the hay and
around it are greater in both sexes than movements in
the rooms.

Some evidence was collected on the importance of
emigration and immigration between the hay barn
and surroundings. Frequent inspection and occa-
sional trapping of adjacent buildings suggested that
populations in these were undergoing similar changes
and no evidence was found of movement between
them and the hay barn. A hedgerow about 250 ft.
from the barn on the other side of the field of short
grass was trapped in June 1949 and the following
were live-trapped, marked, and released: seven
Peromyscus, two Microtus, one Sorex, one Blarina,
and six Mus. There were no recaptures. It is highly
probable that there was some immigration and emi-
gration between the barn and the fields but there is
no evidence that it was of much importance in this
case. Ground around the barn was thoroughly exam-
ined periodically and traps set around the barn dur-
ing every period. The mouse sign and trap success
were both consistently lowest on the sides adjacent
to the field.

Sex Ratio. An analysis of the sex ratios revealed
by trapping shows that of the 570 mice captured
340 or 60% were males. Of the 418 mature mice
captured, 264 or 63.2% were males. Of 152 imma-
ture mice captured, 76 or 50% were males. The
difference between the sex ratios of the mature and
immature animals is statistically significant (P<.01).

An analysis of the relationship between the per-
centage of males captured and the various population
phases (peak, trough, increasing, decreasing) re-
vealed no satistically significant differences in the com-
position of the population during these different
phases (P>0.20). This is supported by Laurie's
work on house mice in England (1946) where no
significant differences was found in the sex ratio of
house mice living in four different environments
through a period of one year. It is interesting to
note that in a rapidly decreasing house mouse popu-
lation Evans (1949) found an unequal sex ratio
strongly in favor of females. If it were possible
to attach any significance to the sex ratio in decreas-
ing populations in the present study there would
be a ratio strongly in favor of males. Laurie found
the sex ratio to be 1:1 in three of the environments
studied but in grain ricks there was a numerical
superiority of females, (55.39%).

There is a correlation between the size of home
range and the sex ratio as revealed by trapping.
Animals having a large home range could be expected
to come in contact with a greater number of traps
than those with a small home range. Since male
mice exhibited a larger average home range than
females, a higher percentage of male captures was

expected. Because of this difference, although the
sex ratio is significantly different from 50.0%,
(P<.000001), no attempt is made to estimate the true
sex ratio in the population.

The difference between the sex ratio of mature
and immature captures suggests that there may be a
difference in home range between the two groups.
If the true sex ratio of the population were 1:1 and
the home ranges and trappability of both sexes were
the same we would expect male captures to approxi-
mate 50%. If we assume no difference in trappabil-
ity between the sexes it appears from the results
here that the home ranges for both males and fe-
males are similar before sexual maturity and that the
increase in home range in the male occurs after sexual
maturity.

An analys's of the relationship between the number
of animals captured per trap period and the number
of males captured was also carried out. A chi-square
test gave a P greater than 0.30 thus indicating no
statistically significant differences among the different
sizes of captures in the number of males captured.
Seasonal Distribution. The seasonal distribution of
mice in the barn followed a regular pattern for both
years and the data for the two have been lumped
together. An analysis of the percent of total mice
captured that were taken in the hay mow shows
76.0% for the hibernal, 31.3% for prevernal, 28.3%
for vernal, 52.4% for estival, 71.4% for postestival,
71.9% for serotinal, and 64.5% for autumnal. The
autumnal season of 1948 is the one exception to the
pattern with 37.0% of the captures in the hay mow. In
general the pattern shows a marked abundance of
mice in the hay mow during the postestival, serotinal
and hibernal seasons with similar abundance during
the autumnal of 1949 and 1950. A sharp drop oc-
curs in the prevernal and vernal. Although the
difference between the vernal and estival seasons is
not quite significant (P=.06), the steady trend up-
ward from the estival through the serotinal and
hibernal correlates very well with changes in farm
practice concerning the handling of hay in the hay
mow. This change will be dealt with in more detail
later. An additional factor operating in the barn
in the cooler seasons, especially the hibernal, is the
temperature gradient between the cold peripheral
rooms and the warmer hay mow. Although the
abundance of food in the peripheral rooms did not
change appreciably in the fall and winter the
abundance of mice captured and the visible fresh
signs in the peripheral rooms dropped markedly to
the low in the hibernal season. At any time of the
day during this season numbers of mice could be
seen and heard foraging throughout the hay. Un-
fortunately, not enough is known about farm condi-
tions and practices prior to the autumnal season
of 1948 so no explanation is available for the big
difference between this season and the two following
autumnal seasons. There were certain local areas in
the barn, especially around feed bins, where food
was apparently always in abundance. These areas
were focal points of small population concentrations

and were not appreciably affected by climatic conditions in the barn from season to season. They never appeared, however, to reach anything near the maximum utilization of the available food and cover and the problems arising from the factors responsible for the upper levels in those populations were instrumental in establishing the course of the experiments later carried out in the laboratory (Section II).

Daily Activity Rhythm. Results of the analysis of nocturnal and diurnal trap success indicate that mice in the barn showed a tendency toward diurnal activity (Table 8). Trap success for the nocturnal trapping periods was 0.64 while trap success for the diurnal periods was 1.20, nearly twice that of the nocturnal. That this tendency is well established in the population is indicated by the fact that there was only one reversal, during the first vernal season, and it was of small magnitude. It is during the day that the general activity and environmental disturbance reach a maximum in the barn and in spite of this there exists this tendency toward greater activity. Because of the fact that traps were not run at daybreak and nightfall the data err in favor of the nocturnal trap success, some animals active during daylight hours being caught before traps were run in the morning and after they were run in the evening, so the figures presented can be considered a conservative estimate of diurnal activity.

Analysis of the percentage of males that were diurnal and nocturnal shows that 51.2% of the diurnal captures and 62.1% of the nocturnal captures were males, a significant difference in favor of nocturnal trapping ($P=.02$). This suggests that perhaps females show greater "around the clock" activity than males which may be due to the constant demands of pregnancy and lactation. An alternate explanation may be that males active during the daylight operate over a longer period of time, thus exposing themselves to capture in the morning before the traps are run or in the evening after traps are run. There is little evidence, however, to give preference to either explanation.

A breakdown of the percent of immatures for diurnal and nocturnal periods shows a high degree of similarity between them with 27.6% diurnal and 24.2% nocturnal captures. There is no statistical significance between the two (P approximately .36). An analysis of trap success for immatures and matures for nocturnal and diurnal periods was done using trap hours corrected for traps unavailable to each because they were occupied by individuals of the other category. The number of occupied traps was divided by two and subtracted from the total available on the assumption that they were sprung at an arithmetic rate during the period they were set. From this corrected trap success the ratios of diurnal captures to nocturnal captures may be calculated and show when compared that 2.18 matures and only 1.68 immatures were captured. This suggests that there is a stronger tendency toward nocturnal activity in immature animals. Since young mice often spend some time after birth in the darkness of the

TABLE 8. Daily activity rhythm as revealed by trapping.

Season	DIURNAL			NOCTURNAL		
	Captures	Trap hours	Trap success (Captures/ 100 trap hours)	Captures	Trap hours	Trap success (Captures/ 100 trap hours)
Autumnal...	32	2219.5	1.44	76	7359.0	1.03
Hibernal...	23	2793.0	0.82	41	9096.0	0.48
Prevernal...	19	1073.0	1.77	22	2960.0	0.74
Vernal......	10	1948.0	0.51	21	3752.0	0.56
Estival......	3	1845.0	0.16	6	5342.5	0.11
Postestival..	6	539.0	1.11	11	2640.0	0.42
Serotinal....	31	1839.0	1.69	45	5238.0	0.86
Autumnal...	30	1266.5	2.37	27	1715.0	1.57
Hibernal....	32	2630.5	1.22	29	6766.0	0.43
Prevernal...	20	1128.5	1.77	22	2568.5	0.86
Vernal......	5	532.0	1.13	9	1275.0	0.71
Estival......	no data					
Postestival..	no data					
Serotinal....	6	511.0	1.17	7	1277.5	0.55
Autumnal...	7	498.0	1.41	12	1417.5	0.86
Total....	225	18823.0	1.20	328	51407.0	0.64

nest and surroundings, this tendency toward nocturnal activity is not surprising.

Disappearance of Marked Individuals. An indirect method has been used to get some measure of the disappearance curve in the mouse population. This curve is based on the disappearance of marked and recaptured animals in the population. Since the number of recaptures was too low to make seasonal disappearance curves, all the recaptures were lumped together and treated as though all were marked on the same day. All mice recaptured at any subsequent date were known to have been alive during the intervening time and were added to the totals for each time class on the graph, (Figure 4). The numbers for each time class (20 days) were plotted on a semilogarithmic graph and curves fitted by inspection for males, females, and total animals. These curves were extended back to the time of marking to get a base for determination of the median survival. The chief contributing factor to the difference between the number derived by extrapolation and the actual number marked is the length of time between subsequent trapping periods. If the trapping dates had been closer together the extrapolated number and the number actually marked would have been more similar.

Examination of the median disappearance (point at which 0.50 have disappeared) for males and females shows that males disappeared more rapidly than females. The median for males is 40 days and for females 76 days. This difference between sexes is similar to findings for a variety of other mammals and has been recently reported by Davis (1948) for wild Norway rats. The median for the total animals is 50 days. It should be borne in mind that these figures do not take into account seasonal differences and represent only the average for the year.

If it is assumed further that the disappearance curve has the same slope as does the mortality curve

547 mice marked and released
92 individuals recaptured

○ = TOTAL ANIMALS
● = MALES
◐ = FEMALES
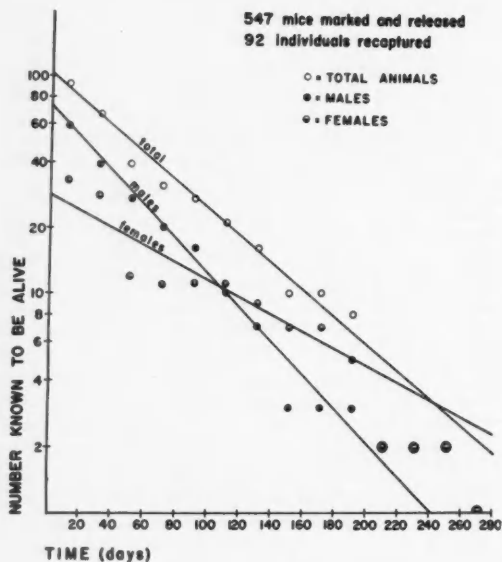
the monthly probability of dying for males is 0.43, for females 0.24, and for total animals 0.35. The similarity between the disappearance and mortality curves is affected adversely by any amount of immigration and emigration, and also by differences in the age-specific mortality rates. Therefore, this estimate of monthly mortality can be considered quite crude at best and only an indication of the magnitude of the differences between the sexes.

Interspecific Relations. Several species of animals preyed upon mice in the barn. During the autumnal and hibernal seasons of 1948-1949 a barn owl *(Tyto alba)* occasionally roosted near the ceiling at one end of the hay mow. Three mouse skulls were recovered from two pellets picked up in November 1948. No pellets were found after this date and no other evidence exists concerning the relations between this owl and house mice. During the estival season of 1949 a stray cat had a litter of four young in the hay mow. She was observed by farm hands to have captured mice but her most conspicuous depredations were on the chicks and ducklings around the farm. It is possible that the low trap success during the estival season was due in part to the activities of this cat. On two occasions short-tailed shrews *(Blarina brevicauda)* were captured in the peripheral rooms of the barn and it is possible that these animals were preying on the house mice. Both shrews were captured during periods when the trap success and signs suggested high mouse population levels. On a few occasions farm hands reported house mice killed by domestic chickens but this is the only information on this form of predation that was collected and no estimate could be made of its importance.

The relationship between Norway rats *(Rattus norvegicus)* and house mice on the farm is of considerable interest since they frequently use the same runways and food supply. The population fluctuations of the two species, while showing similar peaks in the serotinal season of 1949, are elsewhere fairly independent. The chief difference between the species, that of size and speed of movement, sheds considerable light on the population differences. Although both species may use the same food supply, the mouse, because of its small size has access to more of the food stored in bins and can probably survive on a diet of seed from the hay where the rat could not get enough to fill its dietary needs. The mouse, by action and temperament, is quite different from the rat and the amount of conflict between the two species is probably minimized by the ability to avoid direct encounters by rapid escape into places inaccessible to the rat. Because of the difference in size, predation on the rat and the mouse is also quite different. Although the rat and the mouse are the two most abundant mammals on the farm, the competition between them is minimized by these differences in size and activity.

Venables & Leslie (1942) found that in grain ricks in England infested with both *Rattus norvegicus* and house mice there was a partial vertical separation between the two species with the mice found in the lower parts of the ricks and the rats above. They also noted however that high populations of both species sometimes existed in the same rick.

Reproductive Data. Little reliable data can be gotten from the records of pregnancy and lactation recorded at the time of capture. The reliability of the diagnosis of pregnancy is extremely doubtful and most of the pregnancies that had not reached at least fourteen days were missed in the examinations. Since it is almost impossible to express milk from the mammae of female mice under the conditions in which they were handled in the barn this data is also felt to be completely unreliable. For these reasons no attempt has been made to include these data in the analysis. Laboratory examination of large numbers of pregnant mice bred from descendants of the farm mice demonstrated that in many cases only during the last few days of pregnancy did external examination of the abdomen reveal this condition.

DISCUSSION

The factors on the farm that correlate best with the mouse population changes suggested in the barn mice are the changes in farm practice through the seasons. The two most important practices affecting the mouse population are the handling of stock and their food supply. Late in April of each year the cattle and some of the horses in the barn are turned out to pasture for the summer. The hay in the barn has been used and the end result is a sharp decline in available food supply for the mice. This decline in food supply was followed in both years of the study by a decline in the trap success. During the estival season of 1949 there was practically no feeding of stock in the barn and no new hay added to the hay mow. This, coupled with the predation of the stray cat living in the hay mow, correlates very

well with the extreme low in trap success for this season. In the estival of 1950 however the farmer acquired a baling machine and in the early estival season began filling the hay mow with fresh baled hay. Mice were heard and seen in the hay at all hours of the day during this season. In the postestival and serotinal seasons the stock was brought back into the barn at night and fed there. The amount of available food increased markedly and this increase was accompanied by an increase in trap success which lasted through the autumnal season.

The only factor that correlates well with the drop in trap success during the hibernal season is the drop in temperature in the peripheral rooms. As was previously mentioned, the percent of mice captured in the hay increased to a peak during this time. Since the nature of the hay storage area did not permit as complete trapping as the peripheral rooms the trap success for the hibernal season can be considered as a conservative index of the population. Although it is believed that there was some drop in the population during this season, the only information about its magnitude is that the two years were very similar.

The statistically significant differences demonstrated among the various biological seasons are strengthened considerably by the biological implications of these differences. The graphical presentation of the seasonal trap success suggests a regularly fluctuating population with similar timing and magnitude for the seasonal changes of both years. There is evidence that a good correlation exists between these seasonal population changes and fluctuations in the available food in the barn. The biological importance of these seasonal changes are further strengthened by the relationship shown between the number of immature animals captured and the different phases of the regular population changes. It is quite reasonable to expect that marked increases in the number of immature mice in a population would be accompanied by population increase and conversely that a drop in this number would be followed by a decline in the population level.

It appears that this regularly fluctuating population is affected little by immigration or emigration, although this aspect merits considerable further study. Rather than show great mobility and long movements, seasonal or otherwise, the population appears rather sedentary with a restricted home range among the individuals, especially the females. There is a tendency toward diurnal activity suggested in these movements, and this may be the result of freedom from serious large predators. There is little evidence that there is serious large-scale competition between the mice and other animals, especially rats. The most important single factor operating on the population appears to be available food supply.

II. SOCIAL AND REPRODUCTIVE ASPECTS OF POPULATION CONTROL IN HOUSE MICE

The study of the wild house mouse population and its fluctuations on a Maryland farm revealed that although the fluctuations of this farm population appeared to be most closely related to considerable changes in the availability of food, there were local areas in the study barn where food was superabundant throughout the study. These areas were focal points of population concentration of the mice, but nevertheless these small populations never approached maximum utilization of the available food and cover. Since predation was apparently a very unimportant factor in these areas an effort was made to determine what other factors were operating to keep the population level down. Attention was therefore focused on the most conspicuous manifestation of social organization in house mice, i.e., the social hierarchy, and on the reproductive behavior of the adult females. The chief aim was to understand what effect this social hierarchy and reproductive behavior have on the slope and upper asymptote of the growth curve for a house mouse population.

It was necessary to increase the availability of the nests of these mice since they typically build in relatively inaccessible places in the wild. For this reason the mice were moved into the laboratory and the populations under study were housed in large cages. This arrangement made manipulation of the conditions under which the populations lived and observation of mouse activities easier. The basic approach was to set up populations of various densities in closed environments of the same size with ample food and water and observe what occurred in the reproductive and social behavior of individuals in the population.

The social behavior and social organization of groups of inbred laboratory strains of the house mouse have been studied in some detail by other workers. The relationship between fighting and social organization was demonstrated by Urich (1938, 1940). Genetic differences among these inbred strains were shown by Scott (1941, 1942) and more recently by Calhoun (1950b). The hormonal relationships were studied by Beeman (1946) who found a direct relationship between the presence of androgen and aggressive fighting in male mice. Warne (1947) investigated the differences in the amount of time spent in aggregations by the various members of caged groups of mice. A classification of the major types of behavioral responses and a study of territoriality in domestic mice in large pens was made by Scott (1944).

More pertinent to the present study are the works of Crew & Mirskaia (1931) and Retzlaff (1938) on the reproductive rates of mice and their relation to population density. This work, on pregnancy and litter numbers and size, will be dealt with in more detail later. Studies on the response of a house mouse population to restricted food supply (Strecker & Emlen 1950) have a direct bearing on the present study and its relation to wild populations. They found that in a population living wild in a room, the amount of egress from the room increased markedly as food consumption reached the point where all available food was consumed each day. In a popula-

tion that was denied egress when this point was reached, a complete cessation of reproduction followed.

METHODS

The mice used in this study were all descendents of wild brown house mice (*Mus musculus*) captured on a Maryland farm and in the animal rooms at The Johns Hopkins School of Hygiene and Public Health. New individuals from these environments and a small number from a grain warehouse were added periodically. Mice from the school had crossed with escaped albino and black strains from laboratory colonies and a few albinos and black mice appeared in litters.

All mice used in the experiments were descendents of wild animals bred in a stock colony. The mice in the stock colony were maintained in gallon jars with wire lids and watering bottles and approximately two inches of sawdust in the bottom. They were fed exclusively on Purina fox checkers. Jars were cleaned on an average of once a week and food and water were added as needed. Jars containing females with young were not cleaned for two weeks following parturition.

Although breeding of wild house mice has frequently been accompanied by difficulties (Schneider 1946) the farm, school, and warehouse stock reproduced very well. In many of the females a period of acclimation seemed necessary for successful parturition, and, in a few cases, impregnation was delayed four to six weeks. One male and either one or two females were kept in a jar. Pregnant females were isolated a few days before parturition and provided with excelsior for nest material. Young were separated from the females between 25 and 30 days after birth. All albino and black mice were removed from the colony after they were weaned.

All experiments were conducted in large wire cages 6 ft. x 4 ft. x 1½ ft. (Fig. 8). A series of experiments to determine the type of shelter most suitable was conducted. Wooden and cardboard boxes were abandoned as impractical because the mice promptly added several new entrances. The shelter adopted was quart glass jars, placed on their sides and braced to prevent rolling. A triangular hole (one inch on each side) was cut in the metal lids and placed so that the base of the triangle was nearest the cage floor (Fig. 8). Arbitrarily, 1.2 jars per pair of mice were kept in the cages and were spaced equally around the periphery of the cage. The long axis was parallel to the cage wall. No jars were placed in corners. Food was placed in the center of the cage floor and water was available at one side from a glass tube leading to a jar. Unbleached cotton and excelsior were added to the center of the cage for nest material. Food, water, and nest material were added as needed. Cages were never cleaned during an experiment but it was necessary to scrub the jars periodically in order to look inside. The cleaning was usually done without moving the jars and mice inside often appeared little disturbed. A little saw-

dust and nesting material in the jars at the start of each experiment appeared to speed acclimation of the mice to them.

EXPERIMENTAL CAGE

QUART JAR SHELTER
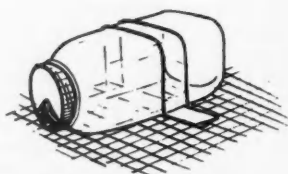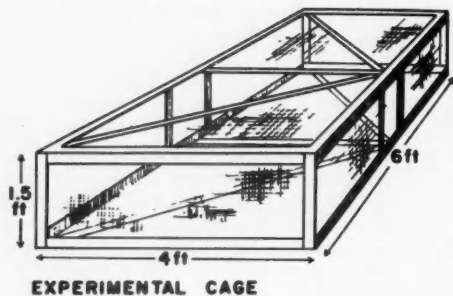
Mice in the cages were weighed and examined periodically. Although an attempt was made to do this once a week, this schedule was frequently upset by events in the cages that required the least possible disturbance. Each mouse, in the stock colony and cages, was individually marked by toe-clipping, and in addition, mice in the cages were individually marked by a red dye (basic fuchsin) for easy identification during observation periods.

Each cage was observed for periods ranging upward of one half hour for a minimum of five hours a week. Light was provided from a single 75 watt bulb and the observer sat about five feet from the cage. A period of ten minutes of quiet before each observation period appeared sufficient to minimize the disturbance to normal routine in the cages. Observation notes were taken in a form of shorthand, and the time was noted on the margin of the observation sheet every five minutes.

Two basic types of experiments were conducted, one on *assembled populations* and one on *growing populations*. The *assembled populations* consisted of multiples of fertile pairs of mice placed in the large cages. All mice used had successfully bred previously and all mice were completely isolated for approximately 25 days before the experiments. *Growing populations* were started with a single mated pair of mice in which the female was visibly pregnant. The population was maintained until successful reproduction had ceased. The mice were then killed and autopsied for reproductive condition. As new individuals were weaned in both types of populations new jars were added to maintain the ratio of 1.2 per pair.

The stock colony was maintained and all experiments were carried out in a room that was heated during the winter and remained close to outside temperature during the summer.

RESULTS

These results are based on observations on 15 assembled populations and six growing populations. The assembled populations were classified into three types based on the duration of the life of the population. Type A was designed to determine the effect of population size on pregnancy and all mice were killed after the experiments had lasted 18 days. Types B and C were designed to determine birth and weaning rates and were run approximately 32 and 60 days respectively. In addition, type C was run to determine the effects of lengthened time in the cages on reproduction. Table 9 shows the number of each type run and the numbers of pairs of mice involved in each experiment.

The most important aspects of these populations dealt with here are social hierarchy, reproduction, population change and incidental social behavior noted in the course of the experiments.

TABLE 9. Physical condition of mice at the end of the experiments on assembled populations.

Exp.	Duration of experiment (Days)	Number of pairs started	Physical Condition at End of Experiment							
			Good		Fair		Poor		Dead	
			Less than 5 Wounds		5 to 15 Wounds		15 Wounds And Over			
			Male	Female	Male	Female	Male	Female	Male	Female
A.1	18	2		2	1				1	
A.2	18	2	1	2			1			
A.3	18	4	1	4	2				1	
A.4	18	4		2	1	2	1		2	
A.5	18	6	1	6	1		3		1	
A.6	18	6	1	4	1	1	2		2	1
Total Animals		24	4	20	6	3	7	0	7	1
Percent of Total Animals			16.7	83.3	25.0	12.7	29.2	0.0	29.2	4.2
B.1	30	2	1	1	1	1				
B.2	35	2	1	2					1	
B.3	30	4	1	4					3	
B.4	35	4		3	1	1			3	
B.5	31	6	1	4	1	2	1		3	
Total Animals		18	4	14	3	4	1	0	10	
Percent of Total Animals			22.2	77.8	16.7	22.2	5.6	0.0	55.6	0.0
C.1	62	2	1	2					1	
C.2	60	4	1	4		1			2	
C.3	45	6	1	4	1	2	2		2	
C.4	69	6	1	3		1		1	4	2
Total Animals		18	4	13	1	4	2	1	9	2
Percent of Total Animals			22.2	72.2	5.6	22.2	11.1	5.6	50.0	11.1

Social Hierarchy. A definite social hierarchy exists among house mice caged together and is determined and maintained to considerable degree by fighting. This was demonstrated by Urich (1938) on a caged albino strain of laboratory mice. He found that fighting was very common among the males, rare between the sexes, and very rare among the females except for a short time after introduction of new females.

Encounters between individuals in both types of experiments in this study that determined or maintained the social hierarchy were of several different kinds and all of brief duration. The commonest was a simple approach-withdrawal encounter between two individuals, one of them dominant. This resulted in chasing by the dominant, but these pursuits were of short duration and seldom lasted over a quarter of a minute. Subordinate animals became so sensitized to this type of situation that as soon as the dominant began chasing one subordinate all the other subordinates would begin to run, and the result was something akin to bedlam. On a few occasions dominant individuals were observed to take food pellets forcibly from subordinate individuals. The most spectacular encounters were, of course, actual fights. These fights were usually brief but frequently furious. This was especially true in the early stages of establishment of the hierarchy before the subordinates became conditioned to the dominant. Severe injury resulted from many of these encounters and examination of the animals after five days together usually revealed subordinate animals with bites about the tail and rump and bites about the head of the dominant. This severe injury to subordinate animals was accompanied by changes in their resting behavior. These animals apparently preferred to remain outside the nests, most frequently on top of the jars where they roosted like birds, able to flee at the slightest sign of aggressive behavior from the dominant. The wounds on some of the subordinate animals became so bad as a result of the constant fighting that almost the entire rump was denuded of skin. These animals were eventually killed if the experiment lasted long enough. If an animal was injured this badly it was unable to escape further encounters quickly and so fell easy prey to the aggression of the dominant. Fights to the death was observed on three occasions and all followed the same pattern. The subordinate was weakened by the repeated onslaughts to the point where it was unable to run and fell over on its side. Every time it moved the dominant returned to attack and the subordinate died within about half an hour of these repeated attacks. On the occasions that subordinate animals did not or could not flee when the dominant approached they typically assumed a stance on their hind feet with one or both front feet raised in front of them. This stance was frequently accompanied by tail rattling in which the tail was vibrated very rapidly against the floor. This tail rattling, however, seems to be a manifestation of extreme excitement and was observed in both dominant and subordinate animals during periods of repeated

strife. On several occasions dominant animals in-dulged in behavior dubbed "making the rounds" in which they deliberately ran around the cage attacking and pursuing briefly every subordinate they en-countered. The deliberate, steady running of the dominants during this type of activity was very characteristic and was readily distinguished from the rapid, jerky movements of other animals in the cage.

The fighting between males in the assembled popu-lations began as soon as males encountered each other after introduction in the cages. For the first hour after the introduction of mice to a cage fighting was extremely intense and as many as 30 separate en-counters were recorded in a five minute period. Af-ter the initial flurry of fighting the number of en-counters tapered off in approximately three days to a much lower plateau.

The social hierarchy in the assembled populations was characterized by a relatively high intensity of fighting throughout the duration of every experi-ment. In all the cages observed there appeared to be a social hierarchy set up in which one male was domi-nant over all other males. Urich (1938) reported that this type of hierarchy was the most common among male albino mice. The intensity of fighting is shown in Table 9 by the high percentage of males killed as the result of fighting and the large numbers in poor physical condition at the end of the experi-ments. Physical condition was determined largely by the number of wounds counted. Good condition meant less than five wounds, fair meant from five to 15 wounds and poor meant 15 wounds and over. The intensity of fighting in the individual cages varied considerably and was related directly to in-dividual differences in the dominants and to a lesser extent among the subordinates. The highest levels of fighting observed depended on the aggressiveness of the dominant but some of the cases of slightly lower levels of fighting were due in part to the aggressive-ness of subordinates. Three cages had subordinates who successfully fought back on occasion but the most successful had only five wins in 23 fights with the dominant. There was no evidence that the sub-ordinates that successfully fought back were inter-mediate in the hierarchy. They were never seen to at-tack the other subordinates once the pattern for the group had been decided. In all cases this pattern seemed well established by the third day and in five cases it appeared to be established within 48 hours.

In the growing populations fighting due to social hierarchy was delayed until the first litter born in a cage reached sexual maturity. In one population there was never any outward manifestation of social hierarchy observed but in the other five there was some fighting. The earliest recorded encounter was between the originally introduced male and a young male 55 days old. Urich (1940) found in albino mice that fighting began on the average at 50 days of age. Fighting was first recorded in the other four cages exhibiting this phenomenon at 59, 62, 65, and 88 days after birth of the first litter. Since these first encounters were of a very sporadic and brief

nature it is very likely that some had occurred previ-ous to the first records. In one cage (C-III) an interesting type of "play-fighting" was observed be-tween young males of the same litter at 33 days of age. This play-fighting consisted of short dashes after each other and pawing and gentle pulling among the three individuals involved. There was no evidence of injury and no individual appeared to dominate the play. This was the only observed in-stance of anything resembling organized play between young mice in the cages. Warne (1947) cites play activity in young groups of house mice (albino) of a somewhat similar nature involving dashing in and out of a specific corner, jumping at each other and pull-ing individuals to a corner of the cage.

In contrast to the social hierarchy in assembled populations, the hierarchy in all but one of the grow-ing populations was characterized by very sporadic fighting of low intensity. Encounters were very brief and "half-hearted" when compared to those in the assembled populations. In all but one cage the originally introduced male remained the dominant individual throughout the experiment. None of the individuals in cages where the originally introduced male remained the dominant showed any serious in-jury from fighting and only one or two bites were ever recorded on any individual. In one cage, how-ever, there was a shift in the social hierarchy and this was accompanied by considerable fighting (C-II). Fighting in this cage was first recorded 88 days after the birth of the first litter and continued at a high level for the duration of the experiment. Seven days after the onset of fighting one of the young males fought and defeated a littermate in a very savage fight. Within twenty days after the onset of fighting this young male, R7, became domi-nant over all but the originally introduced male. The frequency and intensity of encounters gradually in-creased between the dominant and this subdominate and 45 days after the onset of fighting R7 defeated the originally introduced male in a prolonged series of encounters lasting five minutes. There followed a period in which the original male won some of the encounters but lost more and more until 50 days after fighting began R7 was the complete dominant and the original male was a complete subordinate.

Although inter-sexual fighting was uncommon there were some instances in which it assumed importance. In experiment B.3 in the assembled populations a normal dominance hierarchy existed among the males in the cage until about three days before parturition in the females. These four females all gave birth to litters within two days of each other and thus were all at about the same stage of pregnancy. They began to systematically attack the males in the cage, and between the third and last day before parturition succeeded in killing all but one of the four original males, including the dominant. The only male re-maining was the smallest of the four. It is possible that he escaped death through agility in avoiding the heavily laden females. This type of behavior was also observed in experiment C.4 where one of six

females began attacking males shortly before parturition. The fact that these females began attacking when they were all in late stages of pregnancy suggests that this kind of fighting is more akin to defense of the nest than the social hierarchy as is commonly manifested in house mice. In several other experiments females seemed to become directly involved in fighting among males and were treated in somewhat the same manner as other subordinates (Table 9). It is interesting that in the cages in which this was observed there were other females that were never seen to be molested and bore no signs of fighting.

Reproduction. The experiments on assembled and on growing populations were designed to elucidate the relationship between population levels and reproduction. It was apparent early in the study that short duration phenomena such as copulation would require longer periods of observation for each cage than was practical and attention was focused therefore on phenomena either of long duration or predictable as to time of occurrence (such as parturition). During observation periods events relating to pregnancy, nest building, parturition and maternal care of young received the most attention.

In order to determine the relationships between population level and pregnancy a comparison was made between the number of visible pregnancies for (1) the assembled populations and (2) a control group of male-female pairs of mice raised in individual jars (Table 10). In order to keep both groups similar the young born in the jars were removed at birth thus simulating to some extent the loss of litters in the assembled populations. To determine the maximum possible number of pregnancies it was assumed that the females were all impregnated during the first period of heat after parturition. Heat and ovulation are stated by Asdell (1946) to occur within 24 hours after parturition. The number of pregnancies possible for the period spent in the cage or jar was then calculated using 19 days as the duration of gestation (Asdell 1946). As the table shows, the observed number of pregnancies for the assembled populations was 73.2% of the maximum possible number and for the controls was 75.0%, a difference that is not statistically significant (P = .81). Examination of the size of the standard errors for the three different durations of experiments reveals that there is no statistically significant difference among them. It appears that there is little difference between the assembled populations and the control groups in the ability of females to become pregnant. This suggests that there does not exist an effective block to successful conception and pregnancy in populations under these conditions. Due to the number of successful litters in the growing populations and the lengthening of the gestation period during lactation (Snell 1941) it was not felt that a reliable estimate of the maximum possible number of pregnancies could be determined and therefore the growing populations were not included in this table.

A measurement of the number of embryos and

TABLE 10. Comparison of number of observed pregnancies and maximum number possible for the assembled populations and a control group.

Duration of experiment (Days)	Number of females	Number of visible pregnancies	Maximum possible pregnancies	Percent of max. possible observed	Standard error $\sqrt{\dfrac{pq}{n}}$
Assembled populations					
18	24	17	24	70.8	9.3
30-35	18	19	23	82.6	7.9
45-69	20	35	50	70.0	6.5
Total	62	71	97	73.2	4.5
Controls					
18	10	8	10	80.0	12.7
35	10	13	16	81.3	9.8
60	10	18	26	69.2	9.2
Total	30	39	52	75.0	6.0

whole litters resorbed in the assembled populations would be highly desirable but the experiments were so set up that this was impossible. All females that did reach the stage when pregnancy is visible by external examination of the abdomen carried their litters to parturition and the similarity between assembled populations and the control groups of the number of observed and the maximum possible number of pregnancies suggests that the loss of whole litters is not an important factor.

The most important block to successful reproduction in both the assembled and growing populations occurred at or shortly after parturition and involved partial or complete destruction of the litters. This was either by direct killing or by abandonment. Among litters known to have been killed at birth five were from assembled and seven were from growing populations. Among litters surviving birth three from assembled and six from growing populations were killed within 48 hours. From this time up to seven days after birth only one litter from the assembled and three litters from growing populations were killed. No entire litters were destroyed between seven days after birth and the time of weaning. One litter from the assembled and three from the growing populations were abandoned at birth and subsequently died. Two litters from each type of population survived birth and were not abandoned until later. These latter abandonments occurred however before the litters were 24 hours old. In addition to litters in which the cause of death was known there were 27 from assembled and 26 from growing populations which were dead within 48 hours after birth from unobserved causes. A litter was considered successful if at least one individual survived to the time of weaning. In the assembled populations only three or 7.1% of the 42 litters born were successful. In the growing populations 20 or 30.0% of the 67 litters born were successful. Clearly the most important time in the life of the litters is that period within 48 hours after birth, for the loss of litters after this time is very low. This litter loss is

especially pointed up in the assembled populations
by the fact that the three cases that did show repro-
duction were all in the same cage. There was success-
ful reproduction in all of the growing populations.

An indication of the magnitude of survival on the
successful litters can be gained from the history
of ten successful litters comprising a total of 60
young. Each of these litters was observed during the
entire length of parturition. Nine of these 60 young
were killed at birth. Of those surviving five were
killed within 48 hours, four more were killed before
five days of age and three more were killed before
they were 20 days old. Hence, of 60 young born only
39 reached weaning. The average survival from birth
to weaning for the ten litters was 0.65. The fact
that 66.7% of the mortality occurred within 48 hours
after birth emphasizes the critical nature of this
period in the life of the litters.

In all cases where young were killed without being
abandoned the female to whom the litter was born
initiated the killing and consumed the most young.
In many cases parts of the young were left uneaten
and removed from the nest or buried in the nest
material by the sporadic nest building activities of the
occupants. Typically, the mother consumed the pla-
centa and when eating the umbilical cord did not stop
but continued into the abdominal region. The young
were most frequent bitten in half and either the
foreparts or hind parts eaten. Fresh remains were
consumed also by other mice but usually in very
small quantity. There seemed to be no difference
between the reactions of adult males and females to
dead young. In the cases in which the young were
killed after successfully surviving parturition the
killing usually came about as a result of accidentally
breaking the skin during rough handling by the
mother in retrieving or licking the young. In four
cases observed, the female, after consuming the orig-
inally injured individual, turned to the others and
partially consumed each of them.

In the cases of abandonment recorded for the two
types of populations it is not known which mice
consumed the young that were eaten. In the as-
sembled populations a total of three litters were
known to have been abandoned, one of four young at
parturition and two of five and seven respectively
within 24 hours. One of the abandoned litters (seven
yg.) was moved three times by the mother in five
hours over distances of one, six, and four feet from
one nest to another before they were abandoned. Of
the five cases recorded in the growing populations,
one with five young was entirely eaten, two of un-
known initial size had at least one eaten, leaving two
and four respectively, and the other two, also of
unknown initial size, showed no record of being con-
sumed (four and five remained). The litter with four
young was abandoned at birth. In the case of the
five that were consumed, three of the young were
moved from the original nest to a nest four feet
away and two were moved three feet away in another
direction. An adult male, one of the first generation,
was observed carrying one of the young to the first

location but there is no evidence that he was in-
volved in the consumption of the young. In the litter
of five not consumed the female moved them at least
once over a distance of two feet before abandoning
them. The other litters were last seen alive in the
nests in which they were born but were scattered up
to distances of two feet after they died.

The most important factor found directly related
to survival of young in both the assembled and the
growing populations was the condition of the nest
at and shortly after parturition. This nest condition
was due largely to the amount of activity in the nest
area by other mice in the cages. Under ideal condi-
tions, with no interference, the pregnant females
typically built deep nests from the excelsior and
cotton provided as nesting material. These nests
were either bowl-shaped or covered, and with no
outside influence present, the latter was most com-
mon. These covered nests had a small entrance at
one side. When the nests were built in the quart
jars provided for shelter they were located at the rear
of the jar and occupied about two-thirds of the in-
terior. When the nests were built out on the floor
of the cage they were in or near one of the corners.
In the growing populations there was one example of
a departure from this covered type where the origi-
nally introduced female built a very large covered nest
with at least two separate chambers (C-III). This
large nest was later added to by the first offspring
and at its peak in size contained four separate inter-
connected chambers each about four inches in diam-
eter. The whole nest was 15 inches across and five
inches high with three entrances. The other type of
nest used in the cages was the platform type, a simple
layer of nest material in a jar or anywhere on the
floor of the cage.

There were sporadic nest building activities occur-
ring most of the time in both the assembled and grow-
ing populations but the most persistent and vigorous
efforts were those of females in late stages of preg-
nancy. Among 33 females in which the beginning of
nest building was recorded, 81.9% started within
three days before parturition, indicating that the urge
to construct nests comes close to the period when
they are of most use. Among these females 21.2%
started nest building one day before parturition,
45.5% two days before, 15.2% three days before,
9.1% four days before, 3.0% five days before and
6.1% six days before. That this nest building is
vigorous is illustrated by the 156 trips for nesting
material made by one female in an hour of building.
Each trip was over three feet in length. All of these
33 females attempted to build at least bowl type
nests but in many cases were thwarted by the activ-
ities of other mice. When there were other adult
females in the cage, these would frequently be stimu-
lated to join in construction of the nest with varying
degrees of success. Frequently they would remove
one side of the nest being built and add it to the
other side or push a whole wall into the bottom of
the nest. Both males and females would often crowd
into this center of activity and the result of all this

"help" and pushing and crowding from others wreaked havoc on the condition of the nest. Thus, although the original builder, the pregnant female, built toward a well constructed nest, she failed because of outside interference.

The amount of interference is directly related to the size of the population in the cage. When there is only a pair of mice the female seems quite capable of building a covered nest and of defending it, thus keeping the male out. In the six growing populations all the females originally introduced built covered nests before the first litter was born and the male was never seen inside the nest between one day prior to parturition and five days afterward. After the weaning of the first litter however this situation breaks down and the female is apparently not able to keep the others from the nest with any degree of regularity. As a consequence, the quality of the nest is frequently impaired. In the assembled populations, however, this latter condition exists from the beginning of each experiment and only three covered nests were ever constructed, two in the same cage and all in jars.

An important relationship exists between success of a litter and the nest built or occupied before and after parturition. Six pregnant females neither built nor occupied nests before or after parturition. Their litters were not successful. In addition none of the 57 females occupying platform nests had successful litters. Before parturition four of these females built or occupied covered nests, 26 built or occupied bowl nests, 20 built or occupied platform nests and seven built or occupied no nests. Nine of the 29 females occupying bowl nests after parturition had successful litters. Of these, two built or occupied covered nests and seven built or occupied bowl nests before parturition. Of the nests built or occupied by the other 20 before parturition four were covered, 12 were bowls, and four had no nest. Seventeen females were associated with covered nests before and after parturition. The litters of only three of these were unsuccessful. A large number of the females who had litters in platform nests either built or occupied more complex nests originally. It is not known in many cases, however, whether those females occupying more simple nests ever attempted construction of more complex types. In the case of the more complex types, the activity and length of time necessary for construction increased the probability that this building would be observed. The seven females observed occupying no nest and shifting at parturition to a platform and the four changing to a bowl type probably made little effort at nest construction and none of their litters were successful.

The direct relationship between the success and survival of the litter and the type of nest occupied at and shortly after parturition is shown in Table 11. This table not only shows that the survival of the litters increases with the increase in complexity of the nest but also that in the case of the growing populations the average size of the litter weaned increases. Although it is not known whether this difference in

TABLE 11. Relationship between the success and survival of the litter and the type of nest at and shortly after parturition.

Number Weaned	Number of Litters Born									Number of successful litters	Percent that were successful	Survivors per litter
	0	1	2	3	4	5	6	7	8			
Growing populations												
No nest	3									0	0.0	
Platform nest	29									0	0.0	
Bowl nest	13	1	3	1	2	1				8	38.1	2.9
Covered nest	2			2	3	5	1		1	12	85.7	4.8
Totals	47	1	3	3	5	6	1		1	20		
Assembled populations												
No nest	3									0	0.0	
Platform nest	28									0	0.0	
Bowl nest	7			1						1	14.3	4.0
Covered nest	1		1		1					2	66.7	4.0
Totals	39		1	1	1					3		

the number weaned represents a difference in size of litters born or a difference in survival it seems reasonable to favor the latter explanation for there is no indication that the number to be born affects the quality of the nest. For example, of the ten litters of known size at birth previously mentioned six were born in covered nests with an average of 5.8 young and four were bowl types with an average of 6.3 young at birth.

In addition to altering the condition of the nest, the activities of other mice affect the amount of activity of the pregnant female prior to parturition. Under normal conditions females in the late stages of pregnancy are quieter and move about less than nonpregnant mice. This was very obvious in the stock colony where the rack of pregnant females was next to a rack of females isolated after they had been proven fertile and were being held for use in the experimental cages. The only activity of a vigorous nature in these pregnant females were relatively brief periods of nest building. This lack of activity was also observed in the originally introduced females in the growing populations prior to birth of the first litter but was lacking to some degree in pregnant females in cages of higher populations. The amount of jostling due to the activities of other mice is apparently responsible in part for this difference in activity and pregnant females in high populations were frequently seen clinging to the top of one of the walls away from the general area of activity.

The events occurring at parturition are quite naturally of primary importance in determining the fate of the litters. Under ideal conditions of isolation such as were present when only a single pair of mice were in the cage, parturition occurred with a minimum of activity. In isolation the young were usually born several minutes apart with considerable variation in the length of time between deliveries. For example, one female gave birth to six young with the following number of minutes between successive de-

liveries: 21, 12, 4, 14, 4. Between deliveries the females shifted around in the nest or rested quietly between the frequent cleaning and licking of the young. During the birth of the six litters born in isolation in the growing populations the females never left the nest vicinity during the period of parturition. The greatest distance moved was six inches by a female apparently investigating the observer. In contrast to parturient females in isolation, those giving birth to litters under crowded conditions showed considerably more activity between deliveries and often left the nest area completely. This situation was especially conspicuous in the cases observed where the amount of activity by other mice moving in and out of the nest was high. The activities of the other mice determined the extent of the disturbance to the parturient female and her nest and hence affected the success of the litter.

The reactions of these other mice to the young ranged from a general disinterest on the part of the males, which bordered on an actual avoidance reaction, to the excited sniffing, licking and handling of the young by females who were in the late stages of pregnancy or recently parturient. The males exhibited little or no interest in the young and actually appeared to avoid contact with the young on two occasions when they were present at parturition. It was apparent that they were responsible for much less of the disturbance than were the adult females. The excited activities of these adult females ranged from mild interest on the part of nulliparous females to the actual partial usurping of the nest and young by a female that had recently lost her litter. In the latter case the female partially took over the nest and young born to one of her offspring three days after she had consumed her own litter. For a period of seven days both females nursed the young but their activities and those of others gradually destroyed most of the nest and the young were finally consumed on the evening of the seventh day. In four cases observed the nest was seriously altered and destroyed by the nest-building efforts of highly excited females in late pregnancy who were present at parturition. Most of their activities consisted of picking up one part of the nest and depositing it in another part, often on the new-born young. On five occasions females were observed carrying the young around in the nest in an aimless, weaving manner, occasionally putting one down and picking up another. There were only two instances in which males were observed handling young. One, previously mentioned, concerned the male in the growing population observed carrying one of a litter that was subsequently abandoned and the other involved a male seen carrying a newborn mouse from a nest in an assembled population (C.4). This young mouse was later destroyed. The chief disturbance caused by immature animals resulted from their habit of climbing over the young and scattering them or resting on top of them, thereby denying the mother access.

Population Levels. There was considerable difference between the assembled and the growing populations in the manner and direction they took to reach equilibrium. Table 12 gives an analysis of the time of death for individuals in the assembled populations. It can be seen that in all but one the population either remained static or declined. However, since most of these experiments were of very short duration only those in the last group, extending at least 45 days, are used for comparison with the growing populations. In these four populations three declined and one increased after an initial decline.

TABLE 12. Time of death and population size at the end of the experiments in the assembled populations.

Experiment Number	Duration (days)	Initial Pop.	WEEKS IN WHICH DEATH OCCURED				Pop. at End of Experiment
			1-2	3-4	5-6	7-8	
A.1.......	18	4	1	0			3
A.2.......	18	4	0	0			4
A.3.......	18	8	1	0			7
A.4.......	18	8	0	2			6
A.5.......	18	12	1	0			11
A.6.......	18	12	3	0			9
B.1.......	30	4	0	0	0		4
B.2.......	35	4	0	1	0		3
B.3.......	30	8	0	3	0		5
B.4.......	35	8	2	1	0		5
B.5.......	31	12	1	1	1		9
C.1.......	62	4	1	0	0	0	3
C.2.......	60	8	2	0	0	0	6
C.3.......	45	12	0	1	0	1	10
C.4.......	69	12	3	1	1	1	19*

*Successful reproduction.

This initial decline is characteristic of the assembled populations as a whole and is directly related to deaths resulting from the actions of social hierarchy. In contrast, the growing populations all show marked increases (Fig. 6). In all but experiments C-I and C-IV the increases in population were followed by a leveling off which, although short in some of the experiments when they were discontinued, was characterized by no successful reproduction or changes in the quality of the nests built. Since the litter destruction in the cages made it impossible to count all young born, fluctuations due to newborn litters are not shown and increases are figured from the time the litters were weaned. Thus, in C-I for example, the initial increase at 83 days is caused by an influx into the population of a litter of six weaned and active mice, born 20 days previously. The duration of the final plateaus in the growing populations are figured from the birth of the last successful litter and are indicated by the dashed lines on the graphs.

The case of Exp. C.4 in which the initial decline was followed by an increase due to survival of three litters suggests a possible course for some of the assembled populations (Fig. 7). This survival, the only case of successful reproduction in the assembled populations, was correlated directly with the complexity of the nest that the females were able to maintain. The nests built were unusually large and well
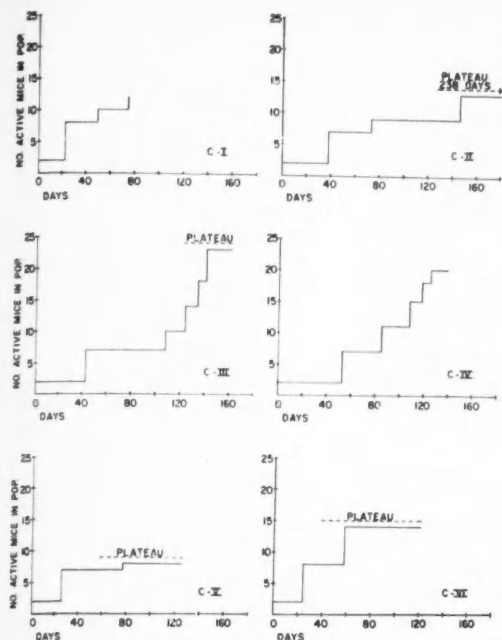
built with thick walls in the two covered nests and very high sides in the bowl-type. The two covered nests were built inside jars but the bowl-type nest was built in a corner. The other mice in the cage showed little inclination to enter or remain in these nests, and it is possible that these females had established exceptionally good nest defense, although no overt signs of this appeared after the young were born.
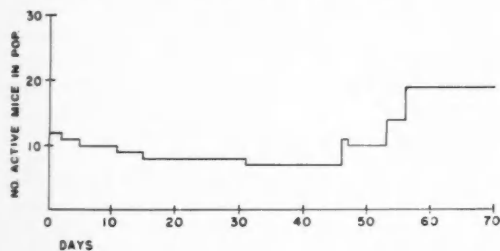
In the case of the litter in the assembled population (six pairs, C.1) that survived seven days the unique association of the mother and a pregnant female appeared to be most responsible for the survival. The litter was born in the back of a jar in a well-constructed, covered nest. The pregnant female occupied the front of the jar near the entrance and at no time during the first five days of the litter's life were both females away at the same time. The extreme caution exercised by other mice when approaching the entrance of the nest jar suggested that these females had established a strong nest defense. This was maintained to the fifth day, when for an unknown reason, the nest was moved three feet to another jar.

This relationship between the mother and the pregnant female appeared to break down at this point and the litter was missing two days later.

The equilibrium reached by the growing populations appears directly related to crowding, but in populations of the size used here the action of social hierarchy was definitely secondary if at all apparent. The pregnant female, when faced with a single adult male, was apparently capable of keeping him out of the nest but this ability broke down when the first litter was weaned. This breakdown seems to be associated with the fact that the litter was raised in the nest, and is closely associated with the female. This relationship is demonstrated by the fact that in 29 observations of the proximity of sleeping mice in a cage containing an adult male and female and a litter weaned at least two weeks previously, the female and the whole litter were together 17 times. The female and male were together four times, and the male was seen with one or another of the litter five times.

By the time the population is composed of several adults the nest defense has been very thoroughly broken down and nest disturbance is at a maximum. It is at this time that the upper level of population is reached. This upper plateau is characterized by no successful reproduction and generally poor nests. Females attempting to construct complex nests never get much of a start before the nest is broken down by others. In the case of C-II the last 78 days were characterized by only platform nests and often none at all. As far as was observed this was also true for the last 45 days of C-V and the last 67 days of C-VI.

The difference in the levels of the growing populations at the end of the experiments is related to the difference in nest building activities of the females and to the amount of interference tolerated in the nest and at parturition. An analysis of these population levels and the types of nests built is given in Table 13. The first four populations are believed to have ceased increasing before the experiments were ended and the last two, C-I and C-IV, may have been still increasing. The fact that C-III had both the highest population when it ceased increasing and also had the greatest number of litters born in covered and bowl nests suggests the nature of this relationship and is supported by the lack of platform nests in the

TABLE 13. Comparison of nests and populations at the end of each experiment in the growing populations.

Cage Number	Nests Prior to Last Successful Litter		Nests After Last Successful Litter		Populations at end of experiment
	Covered and bowl nests	Platform and no nests	Covered and bowl nests	Platform and no nests	
C-V.....	3	1	2	6	8
C-I	3	0	0	0	12
C-II	6	4	0	8	13
C-VI....	2	0	1	6	14
C-IV....	6	0	1	0	20
C-III...	9	4	2	4	23
Total..	29	9	6	24	

still increasing populations. It was in C-III that the large four-room covered nest was constructed. As long as this nest remained intact there was successful reproduction but when the nest was broken in and reduced to a large platform by the activities of the mice successful reproduction ceased. In populations as small as these the addition of a single litter makes a big difference, however, and a much larger series is necessary to conclusively demonstrate the relationship between the population level and nest types.

General Behavior Patterns. The general behavior patterns for mice in both the assembled and growing populations can be conveniently classified into four main types. Arranged in the order of diminishing frequency with which they were observed they are sleeping, investigating, grooming, and feeding. Maternal behavior is not included here because it is confined to the adult females and has already been dealt with in some detail. This is also true for fighting which is largely confined to the adult males. The mice spent a considerable amount of time sleeping, especially during the daylight hours and to a lesser extent in the middle of the night. During the two daily peaks of activity, early evening and just before dawn, the commonest behavior was that of investigation. All parts of the cages were apparently examined periodically by the active members of the populations. This included excursions up the walls and across the ceilings, into and on top of the jars provided for shelter and into and under the excelsior and cotton placed in the center of the cage for nest material. Grooming was also a very important activity at these times and during the daylight hours ranked second to sleeping as the chief activity. Many long hours were spent watching mice in the jars grooming themselves and others. The inter-individual grooming apparently grew out of individual grooming for very frequently a mouse grooming itself would simply shift to the nearest mouse and continue on this individual. This would frequently stimulate the other individual to groom both itself and any neighbor nearby and if there were many mice in the vicinity a veritable epidemic of grooming resulted. Nursing females also spent considerable time grooming the young. Feeding in house mice is a very sporadic type of activity and consists of many short periods of nibbling interspersed with other activities, especially that of investigation. Much food was dropped during feeding and when this was done in the corners of the cage great piles of pulverized food collected in the trays below. Mice were frequently observed carrying food pellets to nests or corners where they could back up against something solid while eating, but there was never any attempt to hoard food.

Mice in the cages showed definite tendencies to aggregate in favorite nests or corners. When there were only a few mice, all would usually be found in the same group but after the number reached about six these were broken down into subgroups. The most consistent groups were of young, mothers and young, and subordinate males, especially those

with severe injuries. Dominant males and females in the late stages of pregnancy appeared to be the least inclined toward aggregation. Warne (1947) working with small groups of caged mice found that dominant individuals spent the least time in aggregations but also spent significantly more time grooming other mice.

Sexual behavior has not been included in the four main types of behavior because it was observed so few times. It most frequently occurred shortly after parturition and was always of relatively short duration. At this time males were seen following the females in heat and repeated attempts at copulation were made, often by several individuals. There seemed to be little relationship between copulation order among the males and their position in the social hierarchy. Unless the individual was frightened away by the approach of a dominant, he could attempt copulation. Reaction of the females ranged from complete tolerance to rather violent attacks on males attempting copulation. The latter reaction was most frequently observed toward the latter part of a period of heat after a female had been mounted several times.

The young mice began investigation of the nest and surroundings actively at about the time their eyes opened, typically about two weeks after birth. At first, they confined their activities to the nest but by the 16th day were exploring cautiously as far as three feet from the nest along natural runways such as the edge of the cage. They were sometimes dragged from the nest by the rapid departure of the mother. If this occurred before they had opened their eyes the mother retrieved them but after their eyes were open they returned unaided. This dragging from the nest may well be one of the important ways in which their knowledge of the surroundings are first acquired. By the time they were weaned, approximately 20 days, they had explored the whole cage and although they spent most of their time in the nest they were often seen in other parts of the cage.

Discussion. Previous workers on the social and reproductive aspects of population control in house mice have concentrated their efforts on the territorial and physiological aspects of the problem. Scott (1944) working on the social behavior, range and territoriality of inbred stocks of agouti and black strains of house mice in large multiple escape pens concluded that the house mouse does not exhibit any definite territoriality. When considering the fluctuating home range and this lack of territoriality Scott concluded that the species has no regular social means of limiting numbers. He further suggested that "the natural controlling factors of mouse population appear to be chiefly ecological, consisting of disease and predators." Crew & Mirskaia (1931) and later Retzlaff (1938) studied the reproductive rates of albino mouse populations established experimentally in small cages. They demonstrated that as the populations were increased from one through twelve pairs there was a gradual decrease in the reproductive rate and average litter size. Crew & Mirskaia found a

decrease in litter size from 7.25 for single pairs to 5.82 for twelve pairs. Retzlaff found a decrease from 7.85 for single pairs to 6.41 for twelve pairs. In both studies pregnant females were removed from the populations shortly before parturition. The results of these experiments do not elucidate the possible different effects of population density on the young and Crew & Mirskaia suggested that the mouse could not be used for this kind of study because under conditions of crowding the young were eaten.

In the present study, the role of disturbances to pregnant and parturient females and their relationship to successful reproduction suggest one social means of limiting numbers in house mouse populations. Under conditions of limited space the crowding of mice becomes of sufficient importance to severely limit and finally halt successful reproduction. It appears that the isolation of the female and her nest from the activities of other mice, especially her previous litters, is important in the successful weaning of the litters born.

The partial or complete breakdown of nest defense appears to be one of the key factors in subsequent litter destruction and hence population control. The experiments on both types of populations suggest that when the female is confronted with small numbers of mice, such as one or two adult males, she can successfully defend the nest. A possible example of extremes in this nest defense is the killing of three males by the four pregnant females in the assembled population B.3. It seems likely that this nest defense would be enhanced by those factors tending to isolate or limit access to the nest. It would therefore be very desirable to initiate a series of experiments in which degrees of isolation of the nest from the rest of the population were varied and the effects on litter success recorded.

When the first litter is weaned in the nest and remains closely associated with the female the probability of survival of the second litter is lessened. The female mice in this study showed no evidence of being able to limit or curtail the activities of the weaned young in the nest and their activities caused serious inroads on the nest condition and increased the possibility of litter destruction by the amount of disturbance they created. This disturbance factor is further intensified when the litter reaches sexual maturity and the reactions of the mice, especially the adult females, create even more disturbance. Their attempts at nest building, apparently stimulated by those of the pregnant female and their reactions to the young severely hinder the successful culmination of the series of events leading to successful parturition and later weaning. Most pregnant females observed did not begin to actively work on nests until about four days before parturition and all litters that survived beyond seven days from birth were successful. Therefore, this disturbance factor is most important for a period of about 11 days, with an upward gradient in the importance of its effects toward the time of parturition.

The probable role of social hierarchy is that of increasing the amount of disturbance. Subordinant animals fleeing the dominant animal were frequently observed taking refuge in the nests. This is complicated however by the change observed in the behavior of those subordinates that were severely injured which resulted in an apparent preference to remain outside of the nests, most frequently on top of the jars. Retzlaff (1938) reports that in his experiments on small populations in cages there was considerable fighting among the females, especially following a new introduction, a phenomenon not observed in these experiments. Most of the fighting observed here among females and between females and males occurred in the assembled populations and may be considered as examples of nest defense. The roles of social hierarchy and of nest defense are undoubtedly interrelated and those females exhibiting dominance are probably better able to defend a nest. This is suggested by a study of Norway rats by Calhoun (1950) on the role of the distribution and availability of food to an increasing population. He found that those animals living nearest the central food supply in a large pen (1000 sq. ft.) were higher in the social hierarchy than those on the periphery and although the number of pregnancies were the same in animals from both areas those nearest the food supply weaned considerably more litters. It is possible that nest defense and social hierarchy among the rats combined to decrease the disturbance to the nest and young.

This study indicates the importance of social hierarchy and the role of disturbances to litter survival in the natural population control of the house mouse living in certain kinds of environments. Under conditions imposed by limited space but abundant food, such as exist in rooms where foodstuffs are stored, the disturbance factors may achieve considerable importance, as they did in the closed environments used in this study. Under these conditions the chief role of the social hierarchy would appear to be that of increasing this amount of disturbance and to possibly aid in the removal of adults through fighting. In environments in which the distribution of food is the important environmental factor and space is more or less unlimited, such as around feed bins in the hay barn of the present study, social hierarchy may also operate as a dispersing agent on the population. In this situation the competition for proximity to the food source may take on aspects of social hierarchy, especially among males, and may involve the success of nest defense among adult females. Social hierarchy may be thought of as playing a double role in natural population control, that of increasing the disturbance factors affecting litter survival and that of a dispersing force, especially on the adult males. The relative importance of the two roles may depend on whether space or food is the chief limiting factor.

Differences in the home range and movements of male and female mice in the farm population may be due in part to the operation of social hierarchy as a dispersing force. There is little doubt that such a social hierarchy existed in the population in the barn

because on several occasions fighting and pursuit between male mice were observed. Those individuals involved in the action of social hierarchy could be expected to exhibit a tendency toward longer movements, greater home range, and possible shifting of the range. This would be especially true among subordinate mice who were in direct competition with established dominants. The suggestion of shifting home ranges among males in the barn may be related to shifts of subordinate mice away from areas where the intensity of the action of social hierarchy is too high. The similarity of the sex ratio of immature animals captured and the difference between it and the sex ratio of adults captured may be directly related to the time of onset of social hierarchy. As has already been suggested, animals with large home ranges could be expected to come into contact with more traps and hence increase the possibility of being captured. If social hierarchy was the chief factor involved in the differences between the home range of males and females it could only be expected to operate as such after sexual maturity. Immature animals, which exhibit few overt signs of hierarchy, would be expected to show no differences in home range. If it is further assumed that there was little difference in trappability between the sexes and that the true sex ratio was something approximating 1:1 in the farm population, we could expect to catch equal numbers of immature males and females, as was the case. It appears that the farm mouse population may consist of at least two slightly different components, the more stable female portion with small home ranges and the more fluid male portion exhibiting a greater range of movement because of social hierarchy. There also exists the possibility of a third component, the immature males and females, both exhibiting the same home range.

It is believed possible that the combination of the effects of social hierarchy and disturbances to reproduction was the chief means of population control operating in the local areas of population concentration surrounding the feed bins. The action of social hierarchy would tend to disperse the mice once they had reached sexual maturity and the disturbances to reproduction would act to cut down the rate of successful reproduction, especially in those females who had recently weaned young. In this manner forces would be in operation from birth to adulthood tending to reduce the population, first operating on the survival of the young and then operating on the dispersal of the survivors. The intensity of the action of these factors would first be seen in the changes they would make in the slope of the curve of population growth and finally, as they reached maximum effectiveness, would be responsible for the determination of the upper asymptote of growth for the population.

SUMMARY

This study of the interrelations of social behavior, reproduction, and population changes in the house mouse (*Mus musculus*) was undertaken in an effort to understand some of the aspects of natural population control in this species.

The initial phase, study of a population of house mice on a Maryland farm, was carried out by live-trapping, marking, and releasing individuals at least once a month from November 1948 to October 1950. Population levels were estimated by a trap success index (mice-per-100-trap-hours). There was a marked similarity between the two years in mouse population fluctuations. These were correlated with changes in farm practices. The population appeared to be regularly fluctuating with peaks in the prevernal (early spring) and autumnal seasons and troughs in the hibernal (winter) and estival (summer) seasons. Mice were classed either as mature or immature based on their weight and reproduction condition (i.e., immature 12 grams or less, mature over 12 grams). Immature mice were most abundant during increasing and peak phases of population change and declined during the decreasing phase to a low in the trough phase. Analysis of recapture data revealed a greater range of movements and some tendency toward shifting ranges among males. The trapping sex ratio of 50% males for the immature mice was significantly different from the mature percentage of 60.8. No seasonal differences could be demonstrated. There were local areas of superabundance of food which supported local population concentrations throughout the period of study. Nocturnal and diurnal trapping results showed some tendency toward higher activity in the latter. The disappearance rates for marked individuals in the population approximated a geometric decline and the median disappearance for males was 40 days and for females 76 days. The most important factor affecting the general population appeared to be seasonal changes in available food.

Twenty mouse populations of various sizes were established in cages that were 6 feet by 4 feet by 1.5 feet and were observed for a minimum of five hours each week. Two types of populations were used: *assembled populations* of groups of several fertile pairs introduced together and *growing populations* of single fertile pairs allowed to reproduce until successful weaning of young ceased. The social hierarchies established in both populations were maintained chiefly by fighting. This was serious in the assembled populations, and many mice were killed. In growing populations fighting was sporadic and of low intensity, beginning when the first litter reached sexual maturity. In both populations the amount of disturbance created by other mice to parturient females resulted in a decrease in the successful weaning of litters. Although most females attempted construction of either bowl-shaped or covered nests, only 49 of 72 attempted remained in the original condition at parturition, a direct result of the activities of other mice in the nest. Litters of at least one young were weaned from 0.0% of 57 platform nests, 31.0% of 29 bowl-shaped nests, and 82.4% of 17 covered nests. When the disturbance factor introduced by other mice reached a high enough level, all successful weaning

of litters ceased; and the population growth ceased. Litter destruction was principally by the parturient females and consisted of either eating or abandoning the young. Since fighting due to social hierarchy and nest destruction by the activities of other mice were the most conspicuous factors limiting the growth of caged populations it is suggested that these factors may operate in other natural environments. Social hierarchy would tend to disperse mice in open environments and combined with other disturbances in closed environments would decrease successful weaning of litters. The intensity of operation of these factors could determine the shape and upper asymptote of mouse population growth curves under these conditions.

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VEGETATION AND MICROCLIMATES ON NORTH AND SOUTH SLOPES OF CUSHETUNK MOUNTAIN, NEW JERSEY[1]

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INTRODUCTION

Exposure-induced differences in vegetation are widespread and interesting ecological phenomena. Vegetation differences on adjoining north and south slopes may appear as striking alternations of desert shrub and forest (Billings 1951) or as more subtle differences resulting from shifts in dominance or changes in the numerical importance of the species on the different exposures. Braun (1935, 1950) discussed this subtle segregation in forest vegetation in the southern Appalachian Mountains.

Various environmental differences have been found associated with exposure-induced differences in vegetation in the United States (Turesson 1914; Gail 1921; Shreve 1922, 1924, 1927a; Bates 1923; Platt 1951; Parker 1952, among others). In general, it has been found that north facing slopes may differ from adjoining south facing slopes in soil and air temperature, soil and atmospheric moisture, light intensity and wind velocity.

Considerable information has been published on various aspects of the segregation of vegetation in response to changes in slope exposure and on some of the environmental differences found to contribute to the phenomenon, however, much remains to be done. Quantitative studies considering all layers of the vegetation will help to picture more of the subtle

differences that have as yet received little notice. More complete environmental studies considering all seasons of the year may yield information on the causes of segregation. Such environmental data need to be analyzed in terms of conditions during all phases of the life cycles of the plant species which segregate on slopes of different exposure.

The aims of the present study were first, to make a relatively complete analysis of the plant communities found on adjoining north and south facing slopes. Second, to study during all seasons of the year, the nature of the microclimatic layers on the two slopes and to determine the magnitude of the differences in microclimate between the slopes. Third, to investigate some of the periodic vegetational and species phenomena on the two slopes, and to analyze the observed differences in periodicity in the light of the seasonal changes in the environmental differences between the slopes. It was hoped that such a study might indicate critical seasons of the year for at least some of the segregating species and possibly suggest critical ranges in the environmental complex.

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DESCRIPTION OF THE AREA

The study was made on a ridge in the Piedmont of
central New Jersey. The study area is approximately
4 mi. east southeast of Clinton, New Jersey, the geo-
graphic coordinates being latitude 40° 38′ N and
longitude 74° 49′ W. The average elevation of the
top of the ridge is approximately 700 ft. above sea
level, while that of the surrounding area is around
100 ft. Geologically, the area studied may be de-
scribed as a diabase ridge which had its origin as a
volcanic intrusion into the Triassic Red Shales of
the Piedmont. With subsequent uplift, the more
easily erodable red shale was removed, leaving the
resistant diabase dike as a ridge (Lewis & Kummel
1915). The ridge is roughly horseshoe-shaped, the
open end lying toward the east. The valley within,
as well as the surrounding country to the north and
east, is red shale. The study area includes only the
north arm of the ridge, the slopes of which face al-
most due north and south. The slope angle on the
study areas is approximately 20 degrees. Through-
out this study the north facing slope is called the
north slope and the south facing slope is called the
south slope.

The soils on the area studied are residual soils de-
veloped from the weathered diabase. The U.S.D.A.
Soil Survey has classified them as Montalto stony
loam (Patrick et al. 1920). These soils belong to the
gray-brown podzolic soil group. The degree of stoni-
ness varies from place to place over the ridge and
in some areas large stones almost completely cover
the surface. In general, the upper north slope has
more patches of stone covered surface than the up-
per south slope. Although the soils are geologically
quite similar, minor differences may be present due
to the effect of slope exposure.

The general climate of the surrounding region may
be approximated from the 38 year records at Flem-
ington, New Jersey which is 10 mi. south of the
area and has similar topography and elevation. The
average January temperature is 30.8° F, July aver-
age 74.8° F, annual maximum 108° F, and the mini-
mum –18° F. The average date of the last killing
frost in spring is April 24 and of the first in fall,
October 21. The average growing season is 180 days.
The average annual precipitation is around 44 in.,
almost evenly distributed through the year (U. S.
Dept. Agr. 1941). It should be strongly emphasized
however, that the climates of the slopes vary in sev-
eral respects from that characterized by these data.

The vegetation of the region is most closely related
to the oak-chestnut forest of American plant geog-
raphers, in fact Braun (1950) includes the area in
the glaciated section of the oak-chestnut forest re-
gion. The more level terrain surrounding the study

area, upon release from disturbance, may support
fairly good forests composed of *Quercus rubra, Q.
velutina, Q. alba, Q. prinus, Carya tomentosa, C.
glabra, C. ovata, C. cordiformis, Acer saccharum, A.
rubrum, Fagus grandifolia, Fraxinus americana,
Nyssa sylvatica, Tilia americana, Ulmus americana,
Cornus florida, Ostrya virginiana, Carpinus caro-
liniana,* and other species. A few small stands con-
taining these species are present in the general area.

Although early descriptions of the vegetation of
the region, as summarized by Schmidt (1945), indi-
cate many of the above species were present in the
original forests, the relative abundance of these and
other species has changed. The chestnut has been al-
most eliminated by chestnut blight, and the hickories
and white oak have been reduced in importance due
to clearing, burning, selective cutting, increased dam-
age from insects and diseases and localization of
game concentrations. Species that appear to have
increased in abundance as a result of these and other
factors are *Fraxinus americana, Sassafras albidum,
Celtis occidentalis, Juniperus virginiana, Quercus
prinus,* and *Acer rubrum.*

Over the complex intermingling of the many spe-
cies in the area, further complicated by differential
responses to disturbance, lies the modifying and se-
lecting action of topography. Slope exposure, one
aspect of this topographic selection, produces changes
in vegetative composition by effecting a segregation
of the species. Thus, the plant communities on the
north and south slopes, though superficially similar,
are in reality quite different. Statistical analysis of
samples from different slope exposures clearly shows
a marked degree of segregation.

REVIEW OF THE LITERATURE

The literature on the effect of slope exposure upon
climate, microclimate, light, soil condition and plant
and animal life is widely scattered. No studies are
known to the author which attempt to investigate the
complex of interrelationships between all these
factors. Many of the early investigations on slope
exposure were carried on in Europe. Braun-Blan-
quet (1932) mentioned the work of de Candolle
(1856) and Sendtner (1854) on the relationship of
slope exposure to the altitudinal limits of species.
Abbe (1905) reviewed the work of Wollny (1888)
who studied the influence of slope exposure on soil
temperature under various soil cover. He reported
differences in soil temperature between north and
south exposures to be as high as 3° to 4° F at a
depth of 15 cm. Rübel (1908) pointed out that the
total light on a south exposure may be 1.6 to 2.3
times as great as on north exposures.

More recently, Braun-Blanquet (1932) described
the differences in vegetation on north and south
slopes in the Swiss Alps. He has pointed out that
the "heliophytes and light loving communities" reach
their highest limits on south exposures. A consider-
able portion of the more recent European literature
on studies of slope exposure has been reviewed by
Geiger (1950). Generally speaking, his review indi-

cates results similar to American studies.

Studies of the influence of slope exposure on vegetation in the United States have been carried out for the most part in the west. Plummer (1911) found that the percent of surface area shaded by chaparral vegetation in California was lower on south facing slopes than on any other exposure, while it was generally highest on north slopes. Blumer (1911) working in the southern Rocky Mountains found that the distribution of many plants shifts from north to east or west slopes and in many cases even to south slopes with an increase in altitude. Billings (1951) states that this is common with trees in the Great Basin.

Turesson (1914) found that in the arid parts of Washington, slope exposure acted to control the distribution of Douglas fir. Gail (1921) also studied the distribution of this species in reference to slope exposure. In Idaho he found that northeast slopes support forest vegetation while south slopes are treeless. His study revealed that the south slopes had greater wind velocities, an average of 22% lower relative humidity, 50% more evaporation, 44° F greater air temperature range, and that the soil at a depth of 6 in. was below the wilting coefficient three weeks longer than on the north slope.

Shreve (1922, 1924, 1927a, 1927b) in a series of studies in the western United States found the vegetation to be markedly affected by slope exposure. He pointed out that slope exposure determines the temperature of the soil, the "march" of soil moisture and the air temperature. He concluded that insolation is more important than air temperature in determining the temperature of the soil and that the differences in vegetation on north and south slopes are due to a group of conditions initiated by differences in insolation and soil temperature.

Bates (1923) studied the influence of slope exposure in determining forest type in Colorado. He found Douglas fir on the upper north slopes, Engelmann spruce on the lower north slopes, and western yellow pine and some young Douglas fir on the south slopes. His study of environments indicated that the temperature of the soil surface, which reached 150° F on the south slopes, may limit the less heat resistant seedlings. In a later study (Bates 1926), he found that even in the low topography of the Nebraska Sand Hills, there is considerable difference between north and south slopes in the success of tree establishment. Vestal (1920) has pointed out that sites of prairie openings in forest are often south and southwest slopes of valleys where insolation and dry southwest winds produce local xerophytism.

Parker (1952) studied the distribution of tree species as related to slope exposure and microclimate in northern Idaho. He found *Abies grandis* and *Thuja plicata* were more abundant on north slopes while *Pinus ponderosa* and *Pseudotsuga taxifolia* were more abundant on south slopes. From his environmental studies he noted soil temperatures as much as 20° F higher at 3 to 6 in. depth on south slopes as compared with north slopes. He also found relative humidity as much as 25% lower, air temperatures near the ground higher and wind velocities generally greater on south slopes. Soil moisture was found to drop to the wilting percent sooner on the south slopes.

Cottle (1932) found the vegetative cover to be more than twice as great on north slopes as on south slopes in southwestern Texas. He stated that several factors interact to produce this, water relations being the controlling one. On south slopes, he found the soil moisture to be 5 to 16% less, evaporation 24 to 44% greater, soil temperature 10° to 20° F higher at a depth of 2 in., atmospheric humidity 5 to 11% lower and wind velocity greater. The study included the growing seasons of three years.

Some study has been made of slope exposure effects in the eastern deciduous forest. Harshberger (1919) described vegetation differences in eastern Pennsylvania due to slope exposure. Potzger (1935, 1939, 1950) and Potzger & Friesner (1940a, 1940b) investigated the vegetation of central Indiana as related to slope exposure. They reported a marked segregation of species on the two exposures with the result that beech-maple forest with its understory occurs on north slopes and oak-hickory with its understory occurs on south slopes. In one study (Potzger 1939), the soil moisture was found to be below the wilting coefficient more frequently and for longer periods, and evaporation and air movement were found to be greater on south slopes. These authors emphasized the relative stability of this north-south slope segregation.

In Iowa, Aikman & Smelser (1938), Aikman (1941) and Aikman & Brackett (1944) discussed the influence of slope exposure on natural vegetation and cultivated plants. They found forest communities to possess different structures on the two exposures. In regard to environment, they reported that slope exposure influences evaporation, soil and air temperature, daily temperature range, number of freeze-thaw cycles, air movement, and air drainage.

In the southern Appalachians, Braun (1935, 1950) emphasized the segregation of species and plant communities as a result of slope exposure. In the mid-Appalachian shale barrens, Platt (1951) found slope exposure ". . . critical and absolute in the formation of (these) shale barrens. On moderately steep slopes barrens have been found only on those areas having a southerly exposure." He found a maximum surface temperature of 63° C on one south slope and came to the conclusion that such temperatures plus other factors related to exposure were important in determining the composition and general aspect of the vegetation on the barrens areas.

Shanks & Norris (1950) described the segregation of species on north and south slopes in a small valley in eastern Tennessee. They reported that species in all layers of vegetation show certain degrees of restriction to one or the other exposure. In their study, mean air temperatures at one foot were found to be 3° F higher on south slopes while the maximum air temperatures were 11° F higher. They found that

the differences in minimum air temperatures were generally less than 1° F between the slopes.

Foresters have been concerned with the effect of slope exposure upon forest fire danger and damage. Hayes (1941) pointed out that forest fire danger is almost always greater on south exposures where the duff, litter and other fuel are drier. He found that in Idaho the difference in fire danger between the slopes decreases during mid-day and with altitude. Byram (1948) discussed the role of terrestrial radiation in maintaining high moisture content in forest fire fuels on north slopes. He pointed out that the lower surface temperatures operate to keep moisture content higher on this exposure.

Boyko (1945, 1947) discussed the role of the insolation-exposure factor in determining forest type. He stated that in the southern Mediterranean region several species may shift from a predominantly southern exposure near the coast to a northern exposure further inland.

Slope exposure has also been shown to affect the life form spectrum and plant succession. In North Carolina, Oosting (1942) found south slopes to have greater numbers of therophytes while north slopes have greater numbers of cryptophytes. Daubenmire & Slipp (1943) suggested that winter conditions, such as snow accumulation, may be more important than growing season differences in temperature and moisture in influencing plant succession on talus slopes in northern Idaho. Shaw (1916), in describing the vegetation of the Selkirk Mountains, also emphasized the importance of winter differences on slopes of different exposure.

Thus, this partial review of the literature indicates that studies of the influence of slope exposure on vegetation have been made in widely different climatic regions. No attempt has been made to cover the literature for the southern hemisphere. For the northern hemisphere, certain generalities can be drawn from these studies concerning the influence of slope exposure upon the environment. However, generalities concerning the influence of slope exposure upon vegetation cannot be made. Regional climate, differences in species and our general lack of understanding of the complexities of vegetation dynamics prohibit this.

METHODS

THE MICROCLIMATE

The study of the environments of the two slopes was primarily an investigation of temperature and moisture in the microclimatic layer and of soil temperature. The microclimatic observations were obtained for the most part from two pairs of stations on each slope. These stations were situated about 60 m in linear distance below the crest of the ridge. The two stations on each slope were approximately 25 m apart. The first station established on each slope was situated in a location that was selected as being representative of the largest area of the community on each slope. These two locations were in areas away from the trunks of trees and the tree cover overhead was

as near alike as was possible to obtain and still keep the site typical of the slope. Though the species contributing to the canopy were not the same, the amount of cover was approximately the same, the north slope having slightly less cover. During June, when the sun was near the summer solstice, both stations received some direct insolation at the forest floor. These stations were designated N-1 and S-1 on the north and south slopes respectively.

At the start of the second year of observations (May 1949), it was noted that two trees which had contributed to the canopy above the south slope station during the first year had died. The canopy directly over the instruments however, was still fairly complete. Even after this opening occurred, the tree canopy within a radius of 10 m was still heavier on the south slope. The trees which died, however, were located south from the station, and their death influenced the observations made in the microclimatic layer the second summer.

The other station on each slope, established during the second growing season, was situated directly under trees. During the summer, these stations (N-2 and S-2) received little or no direct insolation. Again, the species of trees providing most of the shade were not the same, but the amount of cover was approximately the same.

In addition to these two pairs of stations, temporary stations were maintained on each slope during the spring of 1949 at elevations above and below the permanent stations. At these stations, air temperatures (weekly maximum and minimum) were obtained at the 1-m level.

In selecting levels for microclimatic observations, an attempt was made to sample the atmosphere at heights which correspond as nearly as possible with the vegetation layers. The climate of the terrestrial bryophytic layer is represented by the 5-cm level, the lowest possible level which could be sampled with the type of thermometer shield used. The climate of the herbaceous layer is represented by the 20-cm level, of the shrub layer by the 1-m level, and of the tree layer by the 2-m level. Obviously, 2 m is well below the true tree layer, but higher levels were not studied due to lack of instruments and the increased danger of the stations being discovered and vandalized. The 2-m level was also chosen because it corresponds to the level widely used for gathering synoptic climatic data.

Air temperature observations were made with weather bureau-type maximum and minimum thermometers. Those were exposed in pairs (one maximum and one minimum) in an aluminum shield designed by Dr. C. W. Thornthwaite and his coworkers. The author is indebted to Dr. Thornthwaite of Seabrook Farms, New Jersey for suggesting the use of these metal shields and for supplying six of the ones used in this study. A brief description of these shields has been published by Baum (1949a).

At stations N-1 and S-1, these shields were attached by means of an aluminum band and screws to a post erected for the purpose. All four levels

mentioned above were sampled at these stations. At stations N-2 and S-2, the shields were attached to trees at the 5-cm, 1-m and 2-m levels.

Soil temperatures were obtained with weather bureau-type maximum and minimum thermometers buried at a depth of 4 cm under the soil surface. The soil was removed for each reading and replaced with light hand packing. It was considered impossible to reproduce the duff layer, so this was removed and never replaced. The leaf litter was reproduced as closely as possible after each reading. The 4-cm level was chosen since above this level the ordinary thermometer becomes much more inaccurate (Daubenmire 1943). Below this level, the difference in soil temperature between the two slopes is less.

Atmospheric moisture was determined at stations N-1 and S-1 at the 5-cm, 20-cm and the 1-m levels. Wet and dry bulb temperatures were obtained with a Frieze Model HA/2 hand aspirated psychometer. Determinations were made for the most part around midday.

Air movement was estimated, except that on one day accurate wind observations were made at the various levels with a Hastings air flow meter which has a hot wire as the sensitive element.

The length of records and frequency of observations in the microclimatic study are given in Table 1.

TABLE 1. Summary of the length of record and frequency of observations at the microclimatic stations on the two slopes.

Instrument	Weekly observations	Daily observations
Max-min temperatures Station N-1 and S-1 4 cm under soil	11/ 4/48 – 6/30/49 9/ 1/49 – 2/ 6/50	6/30/49 – 9/1/49
5 cm above soil	5/ 3/48 – 7/ 9/48 9/ 4/48 – 6/30/49 9/ 1/49 – 2/ 6/50	7/ 9/48 – 9/4/48 6/30/49 – 9/1/49
20 cm above soil	5/ 3/48 – 7/ 9/48 9/ 4/48 – 6/30/49 9/ 1/49 – 2/ 6/50	7/ 9/48 – 9/4/48 6/30/49 – 9/1/49
1 m above soil	5/ 3/48 – 7/ 9/48 9/ 4/48 – 6/30/49 9/ 1/49 – 2 /6/50	7/ 9/48 – 9/4/48 6/30/49 – 9/1/49
2 m above soil	12/23/48 – 6/30/49 9/ 1/49 – 2/ 6/50	6/30/49 – 9/1/49
Station N-2 and S-2 5 cm above soil	5/ 6/49 – 6/30/49 9/ 1/49 – 2/ 6/50	6/30/49 – 9/1/49
1 m above soil	5/ 6/49 – 6/30/49 9/ 1/49 – 2/ 6/50	6/30/49 – 9/1/49
2 m above soil	5/ 6/49 – 6/30/49 9/ 1/49 – 2/ 6/50	6/30/49 – 9/1/49
Wet-dry bulb temps.	5/ 3/48 – 7/ 9/48 9/ 4/48 –10/ 7/48	7/ 9/48 – 9/4/48

THE VEGETATION

The composition and structure of the plant communities occurring on the slopes was studied during July and August of 1948 and 1949 using the quadrat method. The size and distribution of the quadrats was the same as has been employed by several previous investigators in the eastern deciduous forest (Buell & Wilbur 1948, and authors cited by them). Base lines were established at approximately the same elevation on the slopes as the microclimatic observation stations. The quadrats were marked off at 10 m intervals on alternate sides of the base lines. The arborescent layer was sampled on 35 10 x 10-m quadrats (3500 sq. m) on each slope. The number of individuals of each tree species over 1 in. d.b.h. and their diameters were recorded. The shrub layer was sampled on the same number of 2 x 8-m quadrats (total area, 560 sq. m.) nested in one corner of the tree quadrats. The number of individuals of each species was recorded. The herbaceous layer was sampled on 140 ¼ x 4-m quadrats (total, 140 sq. m.). Four herb quadrats were nested one in each of the four corners of the 35 tree quadrats. The number of individuals of each species was recorded in each quadrat. In frequency tabulation, the four herb quadrats located in each tree quadrat were combined as a unit resulting in 35 units of 4 sq. m for each slope. The terrestrial bryophyte layer was sampled on the north slope on 50 2 x 5-dm quadrats spaced 2 m apart. On the south slope, due to the very low moss cover, 100 such quadrats were used. The percent cover in each quadrat was estimated for each species of bryophyte.

From these data, frequency (percent of the quadrats on which each species occurred) and density (number of individuals per unit area) were calculated for all species in the arborescent, shrubby and herbaceous layers. From the d.b.h. data obtained, basal area was calculated for each tree species. Total cover and percent frequency were calculated for each species in the bryophyte layer.

Identifications of specimens found in the study area are those of the author except for the Hepaticae. Specimens of all species are on file in the Chrysler Herbarium at Rutgers University, New Brunswick, New Jersey. Nomenclature is that of Fernald (1950) for vascular plants, Grout (1940) for mosses, and Evans (1950) for liverworts.

All vascular plants found growing in the area were classified as to their life form following Raunkiaer (1934). The species were examined in the field to determine the position of the perennating buds. These field observations were checked against the life form designations given the various species by Ennis (1928), McDonald (1937) and Oosting (1942). Life form spectra were constructed on the basis of species present.

Periodicity data were obtained by recording as many dates as possible for such vegetation changes as germination, leaf expansion, first flowering, leaf fall, etc. The date for each phenomenon was based

upon the time when approximately one-half of the individuals of that species showed the event.

Increase of tree diameters (actually change in radial dimensions) was measured using the method and precision dendrometer described by Daubenmire (1945). Three trees were observed on each slope. Measurements were made at a height of 4½ ft. at two points on the trunk of each tree, one on the north side and one on the east side.

RESULTS

THE MICROCLIMATES OF THE TWO SLOPES

The direction of slope exposure produces a difference in the microclimate of the two slopes that is of great enough magnitude to influence plant life. This difference in microclimate results primarily from the difference in the insolation-radiation balance on the two slopes (Byram 1948). Since the slopes face almost due north and south respectively, and have a slope angle of approximately 20°, the difference in angle of midday insolation is great. Figure 1 shows that the angle of midday insolation is 40° greater at all seasons on the south slope. At the winter solstice, the angle is but 5½° on the north slope while it is 45½° on the south slope. Thus, in December, the angle on the south slope is nearly as great as that occurring in June on the north slope.

LATITUDE N 41°

TIME OF YEAR	20° NORTH SLOPE	20° SOUTH SLOPE	LEVEL
ANGLE OF INSOLATION			
DEC. 22 WINTER SOLSTICE	5½°	45½°	25½°
MAR. 21 & SEPT. 22 EQUINOX	29°	69°	49°
JUNE 22 SUMMER SOLSTICE	52½°	92½°	72½°
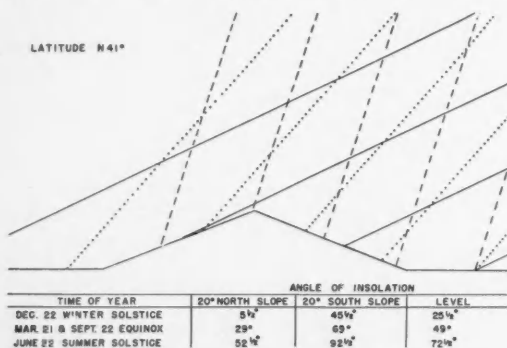
FIG. 1. The angle of midday insolation for the astronomical seasons on 20° north and south facing slopes at latitude N 41°. The solid line is the angle of insolation on December 22, the dotted line on March 21 and September 22, and the broken line on June 22.

Such differences in insolation produce marked effects on the temperature and moisture of the soil and air on the two slopes. During the period of insolation, the climatic differences between the slopes are greater than during the non-isolation period ("period of insolation" is used in preference to "daytime" since all daylight hours may not be insolation hours, especially in a region of sharp relief). This is true since outgoing radiation, as opposed to insolation, is not influenced by slope exposure.

Over the differences in microclimate imposed by the slope exposure itself is spread a mosaic of further microclimatic differences produced by the forest vegetation. Since the forest stand occupying the ridge under investigation is uneven aged and in the process of regaining equilibrium after various disturbances, it forms far from a uniform layer of vegetation. The canopy is uneven and openings of various sizes occur. This unevenness of tree canopy does not permit the complete deactivation of the forest floor described by Geiger (1950). Instead, a mosaic of different microclimates exists on the forest floor dependent upon the character of the canopy overhead.

The influence of openings in the tree canopy on the microclimate below is not the same on the two slopes. As can be seen in Fig. 2, a smaller opening will permit more insolation to strike the forest floor on the south than will do so on the north slope. This results in greater variations in microclimates on the south slope.

NORTH   SOUTH
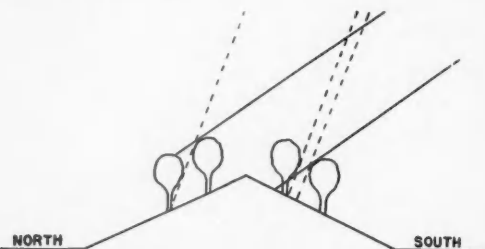
FIG. 2. Influence of openings in the tree canopy on north and south slopes. For the same sized opening in the canopy, more insolation strikes the forest floor, and can penetrate at lower angles of incidence, on south slopes. The solid line indicates an angle of incidence of 35°, the broken line 70° in reference to a level surface.

As previously stated, the microclimatic observations were made at two stations on each slope. The longest records are for the stations on each slope which were chosen as being representative of the greatest area of each slope. On the south slope, the failure of two trees to leaf out in the second summer produced a marked difference in the microclimate at that station. However, the data obtained during the second leaf season are of value since such small openings are widespread on both slopes. During the first year, these stations (N-1 & S-1) received some direct insolation at the lowest level of observations near midday. During the second year, the station on the south slope received some direct insolation at this level from 11:30 to 3:00.

The second stations on each slope (N-2 & S-2) were under heavy shade throughout the day. From spot observations, it was found that areas exist on both slopes where the microclimatic extremes are both above and below those recorded. Such areas, represented by rock crevices, very large openings in the tree canopy, etc., do not occupy much of the area sampled. It seems safe to assume therefore, that the data obtained are fairly representative of the greater part of the area sampled.

TEMPERATURE

The air and soil temperatures were found to be considerably higher on the south than on the north slope. The difference in air temperature between the

slopes is more marked near the surface than at higher levels. This greater difference near the forest floor results from the difference in structure betwen the microclimatic layers on the two slopes.

During the day in the leafless season, the microclimatic layer on the south slope is of the normal daytime type, i.e. with steep temperature gradients, the highest temperatures near the surface (Geiger 1950, Chapman *et al.* 1931, Baum 1949a). During the leaf season the gradient is less marked under shade. Where the shade is heavy, the temperature near the surface may be slightly lower than at higher levels. Geiger has described this condition as due to the deactivation of the forest floor through the interception of insolation and radiation by the vegetation canopy. In relatively small openings on the south slope, a microclimatic structure similar to the normal daytime type prevails.

On the north slope, on the other hand, the usual daytime condition in the microclimatic layer is an inversion, i.e. with decreasing temperature toward the surface. The rate of temperature decrease toward the surface increases with the denseness of the vegetation. The lower air temperature toward the surface on vegetated north slopes is generally attributed to the decreased penetration of insolation near the surface. Since vegetation intercepts considerable insolation, the layer nearest the surface would receive the least. Much of the insolation intercepted by the vegetation is converted into heat which raises the air temperature. Since the lowest layers of vegetation receive less insolation, the air temperature is lower there.

Recently, however, Byram (1948) has suggested a somewhat different interpretation of the daytime temperature inversion which characterizes steep north slopes. He has pointed out that radiation, which is constantly occurring from all surfaces may actually exceed insolation near the surfaces on north slopes. Thus, the forest floor and lower vegetation receive only small amounts of incoming insolation and are constantly losing heat by radiation. These cooler surfaces may then actually absorb heat from the lowest layers of the atmosphere. The air and soil temperatures observed in the present study seem to support Byram's findings.

Since the greatest differences in the microclimatic structure of the two slopes occur during the insolation period, maximum air temperatures should be expected to show the greatest differences. During the twelve month period from May 1948 to May 1949, the maximum air temperatures at station S-1 (light shade) averaged 6° F higher at the 5-cm level than at 1 m. In the second year of observations, the difference at this station was much greater due to the opening up of the canopy as previously described. Only under heavy shade is this temperature profile reversed. From the data for station S-2, it was observed that during part of the leaf season the monthly average maximum air temperature may be as much as 1.9° F lower at the 5-cm level than at 1 m.

On the north slope, the mean maximum air temperature is lower at the 5-cm level than at 1 m throughout most of the year. This is true under both heavy and light shade. The magnitude of this difference varies with the season. The exception occurred in April. Then, before rapid leaf expansion had begun and when the angle of insolation is much increased, the maximum temperature was 3.3° F higher at the 5-cm level than at 1 m. Throughout the rest of the year, the maximum temperature was lower at the 5-cm level, being lowest when covered by snow, as in December, 1948 and February, 1949.

No particular pattern could be found in the distribution of mean minimum air temperatures in the microclimatic layer on either slope. In general, it appears that during the leaf season minimum temperatures near the surface are slightly higher than at 1 m on both slopes. The data, however, are not conclusive on this point. In both 1948 and 1949, during the months of September and October, the mean minimum air temperature was one to two degrees higher at the 5-cm level than at 1 m on both the north and the south slopes. During December and February, 1948-1949 when snow covered the lower level during cold waves, the mean minimum temperature was somewhat higher at the 5-cm level. The north slope data show the snow effect more clearly since the snow remained over the 5-cm level much longer.

Although maximum and minimum air temperatures are of great ecological significance, it is the means which more closely approximate the temperature characteristic of the greater part of the period studied. Mean temperatures are generally obtained by averaging the maximum and minimum temperatures. Although this value has been shown to be inaccurate unless hourly observations are used, the results are probably fairly close under most circumstances.

Baum (1949b) has shown that on level terrain, the higher air temperatures in the microclimatic (as contrasted with macroclimatic) layer during the day are not cancelled by equally lower nighttime temperatures. In other words, the increase in maximum temperature toward the ground is much greater than the decrease in minimum temperature. Baum states that this results in a variation in mean temperature with height which is appreciable. His data indicate that during much of the year the mean monthly air temperature is higher in the microclimatic layer.

In the present study, the microclimatic layer on the south slope was found to show the same general characteristics as reported by Baum. The lowest level of observation, 5 cm, indicates that the mean monthly temperature at this level may be as much as 7° F higher during April than at 2 m (Table 2).

The microclimatic structure on the north slope does not resemble that on the south slope. The mean monthly air temperature at the 5 cm level is lower than at the 2 m level during all months except March and April (Table 2). As stated earlier, this decrease in temperature at the lower levels is probably due to a different insolation-radiation balance resulting from

TABLE 2. Monthly averages of mean temperatures in °F at the levels sampled on the north and south slopes. All values except those starred, including the twelve-month averages at the bottom of the columns, are for the stations under light shade (N-1 & S-1). The starred values are for stations in heavy summer shade (N-2 & S-2).

| Month | NORTH SLOPE | | | | | SOUTH SLOPE | | | | |
| | Soil | Atmosphere | | | | Soil | Atmosphere | | | |
	4 cm	5 cm	20 cm	1 M	2 M	4 cm	5 cm	20 cm	1 M	2 M
May 1948	....	63.2	64.4	64.1	....	....	70.6	67.5	63.9	....
June	....	68.1	69.2	69.1	....	....	70.7	70.1	69.0	....
July	....	72.9	74.2	74.6	....	....	75.4	75.2	75.1	....
August	....	70.0	71.2	71.6	....	....	74.1	74.0	73.6	....
September	....	64.4	65.2	65.1	....	....	72.6	71.1	68.9	....
October	....	51.4	51.6	51.9	....	....	62.4	59.8	56.3	....
November	49.2	50.2	51.0	51.5	....	54.5	59.0	57.4	55.4	....
December	36.0	35.3	35.3	35.5	....	43.0	41.5	39.8	39.0	....
January 1949	34.4	35.9	36.5	37.2	37.2	41.5	41.0	39.2	38.6	38.2
February	33.6	36.2	35.2	36.4	36.8	40.4	42.5	40.0	38.8	37.6
March	38.7	41.3	40.3	40.5	40.4	44.6	47.9	44.5	42.2	41.5
April	47.6	55.1	54.8	53.7	53.6	52.9	60.7	58.3	55.4	53.7
May	57.3	62.2	63.5	63.6	64.0	60.8	69.8	65.5	63.8	62.8
June	63.7	69.4	70.5	70.2	70.3	63.7	72.4	70.5	69.6	69.4
July	71.1	75.2	75.8	76.0	76.1	72.0	78.8	78.4	77.4	77.1
							75.6*		76.4*	76.2*
August	68.9	71.9	72.5	73.0	73.2	72.4	78.1	77.3	76.0	75.1
		71.5*		72.7*	72.9*		74.2*		74.2*	73.9*
September	61.4	61.8	62.4	63.4	63.6	66.4	69.0	67.5	65.6	64.8
		61.2*		62.9*	63.0*		63.7*		64.1*	63.8*
October	55.7	57.7	58.1	59.0	59.1	61.4	66.5	64.5	62.5	61.9
		58.1*		58.7*	59.4*		64.5*		62.2*	61.4*
November	43.4	42.1	43.7	44.4	44.7	49.2	50.6	48.4	46.8	47.0
		43.7*		44.7*	44.8*		52.2*		47.8*	46.8*
December	33.5	33.6	34.6	35.2	35.5	41.8	37.0	36.2	36.1	36.6
		34.0*		35.4*	35.8*		37.6*		37.1*	36.9*
January 1950	35.7	36.5	36.7	37.9	37.8	42.2	41.1	39.8	39.4	39.5
		35.8*		38.0*	38.3*		41.6*		40.2*	40.1*
12 Month Average for 1949	50.8	53.5	54.0	54.4	54.5	55.6	59.5	57.5	56.1	55.5

the combined effects of north exposure and vegetation. The order of magnitude of the difference in mean monthly air temperature between 5 cm and 2 m varies from −2.7° F in January to +1.5° F in April. The higher mean temperatures in March and April occur when the angle of insolation is increased and before the vegetation is in leaf.

With the differences in microclimatic structure described above for the two slopes, it is to be expected that sharp differences in air temperature would occur between the slopes. Furthermore, the difference between the slopes should be greatest near the surface. The data indicate this to be true (Table 3). The data also show a marked seasonal variation in the magnitude of the difference between the slopes. The greatest differences occur in the fall, during the period of leaf fall. In October 1948 the difference in mean air temperature between the 5-cm levels on the two slopes averaged 11° F and in 1949 almost 9° F. The differences are less at higher levels, averaging around 2° F at the 2-m level in October 1949. In May, during the period of leaf expansion, a secondary maximum difference between the slopes occurs. In both 1948 and 1949 the average difference for May was around 7° F at the 5-cm level.

The least difference between the slopes at the 5-cm level occurs during the period when the vegetation is in leaf and the angle of insolation is high. In June,

during both years of observation, the average difference in mean air temperature between the slopes was between 2.5° and 3° F at the 5-cm level. At the upper levels, the north slope actually had slightly higher air temperatures, probably due to the smaller amount of tree cover on that slope.

The soil temperatures 4 cm below the surface are also markedly different between the slopes. These differences show a seasonal pattern that does not correspond with those for air temperatures (Table 3). The differences are greatest when the angle of insolation is lowest and are least when the vegetation is in leaf and the sun is near the summer solstice. The average difference in January is 7° F and in June there is practically no difference between the slopes. This lack of difference is probably due in part to the lower tree cover on the north slope.

ATMOSPHERIC MOISTURE

Since soil and air temperature and atmospheric moisture are closely related, it is to be expected that the two slopes would exhibit differences in atmospheric moisture. Observations of this factor were made during the growing season of 1948. This period was relatively moist and local agriculture experienced no marked drought. The data presented below for midday are based upon 47 observations made at an average time of 12:45 E.S.T. during the period

TABLE 3. Difference in temperature in ° F between north and south slope stations (south minus north). All values are for the stations with light summer shade except the figures starred. The latter are for the stations with heavy summer shade. All figures not prefixed by a sign are positive.

| Month | MEAN MONTHLY DIFFERENCE IN TEMPERATURE IN °F (South minus North) | | | | | | | | | |
| | Soil 4 cm below surface | | Air 5 cm above surface | | Air 20 cm above surface | | Air 1 m above surface | | Air 2 m above surface | |
	Max	Mean	Max	Mean	Max	Mean	Max	Mean	Max	Mean
May 1948	...	...	5.7	7.5	7.8	3.2	1.0	0.4	...	...
June	...	...	4.9	2.6	4.9	1.1	2.0	−0.1	...	...
July	...	...	5.0	2.5	2.7	1.0	1.3	0.6	...	...
August	...	...	7.6	4.1	5.9	2.8	4.2	2.1	...	...
September	...	...	17.0	8.3	13.0	5.9	9.3	3.8	...	...
October	...	...	21.5	11.0	16.0	8.0	9.3	4.4	...	...
November	7.2	7.0	17.8	8.8	13.2	6.4	8.2	3.9	...	...
December	9.2	7.0	16.8	7.3	11.0	4.7	5.0	3.6	1.0	1.5
January 1949	10.5	7.1	10.2	5.1	6.5	2.8	3.2	1.4	1.8	1.0
February	9.8	6.8	15.5	6.8	8.8	4.8	5.2	2.8	2.8	1.1
March	7.7	5.6	13.6	6.2	8.6	3.9	4.2	1.5	1.5	0.7
April	7.0	5.3	11.7	5.6	7.4	3.6	4.0	1.8	2.1	0.1
May	6.2	2.6	14.8	7.6	6.5	2.0	2.2	0.2	0.2	−1.2
June	−0.6	−0.1	6.5	3.0	1.8	0.1	−1.5	−0.8	−1.0	−0.9
July	1.8	0.9	7.7	3.6	5.3	2.6	3.0	1.4	1.8	0.9
			3.8*	1.7*			2.3*	1.1*	1.8*	0.7*
August	5.5	3.5	13.5	6.6	9.8	4.8	6.6	2.8	4.3	1.8
			5.8*	2.6*			3.5*	1.4*	2.8*	1.0*
September	7.1	5.0	14.2	7.2	9.8	5.1	5.0	2.2	3.1	1.3
			5.0*	2.5*			2.2*	1.2*	1.5*	0.8*
October	5.3	4.4	16.9	8.8	11.4	6.4	6.8	3.5	5.1	2.9
			12.7*	6.4*			4.9*	3.5*	2.9*	2.0*
November	6.5	5.9	15.4	8.5	8.9	4.7	4.9	2.4	3.9	2.2
			15.6*	8.2*			5.6*	3.1*	3.4*	2.1*
December	9.3	7.0	7.9	3.0	4.1	1.3	2.7	1.0	1.7	1.0
			7.6*	3.5*			2.4*	1.7*	1.5*	1.1*
January 1950	7.1	6.1	10.1	4.9	6.1	3.1	3.2	1.5	2.8	1.6
			10.9*	5.8*			3.1*	2.2*	2.0*	1.8*
Average for 1949	6.3	4.5	12.3	6.0	7.4	3.5	3.9	1.7	2.3	0.9

May 11 through September 15, 1948. In addition to the midday observations during this period, 8 were made on clear mornings at an average time of 9:00 o'clock E.S.T. It should be pointed out that the morning and midday data are not strictly comparable due to the different number of observations. However, the trend represented by the averages is supported by a comparison of the data from observations of morning and afternoon humidity made on the same day.

In terms of vapor pressure at the dew point (which bears a direct relation to absolute humidity), the midday observations show that the air on the north slope contains more moisture around midday than that on the south slope. The difference between the slopes, however, is not great at either level (Table 4). From the morning observations it appears that during the early part of the day there is slightly more moisture at the 5-cm level on the north slope than on the south slope. At the 1-m level, however, there appears to be slightly more moisture on the south slope at this time. The small number of observations and the small differences do not permit a conclusive statement however.

Both the morning and the midday observations indicate the existence on both slopes of a definite vapor pressure gradient, the absolute humidity decreasing

TABLE 4. The average dew point vapor pressure in inches of mercury at two levels on the north and south slopes. Data for midday are based upon 47 observations made between May 11 and September 15, 1948. The morning data are from eight clear mornings during this period.

| Time | AVERAGE DEW POINT VAPOR PRESSURE IN INCHES HG | | | |
| | North slope | | South slope | |
	5 cm	1 M	5 cm	1 M
12:45 P.M.	.668	.610	.655	.604
9:00 A.M.	.593	.537	.588	.548

with height above the surface. The morning and midday observations indicate that on both slopes there is less moisture in the air at the 1-m level than at the 5-cm level for at least the first half of the day (Table 4).

In ecological studies, it is of interest to know not only how much moisture the air has, but also how much more moisture the air is capable of holding at a particular place and time. Vapor pressure deficit is often used to express this value. The data show a considerable difference in this value between the two

TABLE 5. Average vapor pressure deficit in inches of mercury calculated from the same observations as used in Table 4.

Time	AVERAGE VAPOR PRESSURE DEFICIT IN INCHES HG			
	North slope		South slope	
	5 cm	1 M	5 cm	1 M
12:45 P.M...	.222	.322	.363	.407
9:00 A.M...	.182	.261	.211	.267

TABLE 6. Average wind velocity on the two slopes at four heights above the ground at midday, June 10, 1949.

Height above ground	AVERAGE WIND VELOCITY IN MI. PER HR.	
	North slope	South slope
5 cm..........	0.6	1.5
20 cm..........	0.8	1.8
1 m..........	0.7	2.6
2 m..........	1.2	2.7

slopes (Table 5). As was true with air temperature, the difference between the slopes is more marked near the ground.

A comparison of the average vapor pressure deficits calculated for the two levels indicates that this value increases with height on both slopes. This seems to be true for both morning and midday. The greatest difference in average vapor pressure deficit between the levels was observed on the north slope during midday (Table 5). It is highly probable that if observations were available for the afternoon, gradients would be sharper.

WIND

Observations of wind direction and velocity are based primarily upon estimations. However, even without instrumentation some important points concerning wind on the two slopes can be made. A large number of observations indicate the prevailing daytime wind direction to be up-slope on both the north and the south slopes. This would mean that the prevailing wind would be in the reverse direction on the two slopes. The cause of this situation is the development of eddy currents on the lee side of the ridge and the orientation of the ridge across the prevailing regional summer and winter winds.

Observations of wind velocity based primarily on estimation indicate the south slope to have a somewhat higher daytime wind velocity during the summer than does the north slope. This results from the fact that the prevailing air flow during the summer for central New Jersey is south southwest. Actual measurements made during midday on June 10, 1949 (Table 6) give an idea of the order of magnitude of difference in velocity between the two slopes on a typical day with south southwest wind. Wind velocity was determined at various levels using a Hastings air flow meter. The surface wind direction was south on the south slope and north on the north slope. The average values are presented in Table 6. The wind velocity on that day was more than twice as great on the south slope, and on both slopes wind velocity increased with height above the surface. The data for the north slope show the sharpest change in velocity between the 1-m and the 2-m level. Those for the south slope show the sharpest change between the 20-cm level and the 1-m level. This difference is probably related to the differences in direction of

above canopy winds, wind velocity and the vegetation of the two slopes.

THE VEGETATION ON THE TWO SLOPES

In studying the plant life of an area, it is often useful to distinguish between its flora and its vegetation. Cain (1944) defines flora as being "the plants of an area considered as kinds rather than as composing communities," while he defines vegetation as "the plants of an area considered in general or as communities, but never taxonomically as in floristics." The present study is concerned primarily with the vegetation rather than the flora of the area.

The flora, compiled over three years of intensive study of the ridge, includes 317 species distributed as follows: Tracheophyta 246 including 227 angiosperms, 2 gymnosperms and 17 pteridophytes; Musci 59 species, and Hepaticae 12 species. The only statement that can be made concerning the occurrence of these taxonomic groups on the two slopes is that, in general, there are more species of pteridophytes, mosses and liverworts on the north slope and more species of angiosperms on the south slope.

The vegetation on the area studied is deciduous forest made up of third- or fourth-growth trees under which exist three more or less well defined layers. Although most of the species found on the ridge occur on both slopes, the relative abundance among them, and therefore the resultant structure of the vegetation, is measurably different. All layers were sampled in order to determine quantitatively the nature of this difference in vegetation structure. The quadrat samples on which the study is based contained 175 of the 317 species observed growing on the slopes.

THE TREE LAYERS

There is considerable difference between the slopes in the relative dominance among the species in this layer. There is also a difference in the amount of forest on the slopes as indicated by total basal area. Furthermore, the reproduction of the species is different between the slopes.

The north slope supports a greater total basal area than does the south slope (Table 7). This difference between the slopes is due to the presence of more individuals of the larger size classes on the north slope (Tables 8 & 9). Omitting *Cornus florida*, which never contributes to the upper tree canopy, there are more individuals in all tree size classes on the north slope.

TABLE 7. Basal area by size classes of the trees on each of the two slopes. The values represent the sq. ft. of basal area on each slope per 3500 sq/m.

Species	Indiv. 1.0″ to 3.9″ d.b.h.		Indiv. 4.0″ to 9.9″ d.b.h.		Indiv. 10″ d.b.h. and Over		Total Basal Area on Each Slope	
	North	South	North	South	North	South	North	South
Quercus prinus...............	.136	.005	7.426	4.631	20.309	14.057	27.871	18.693
Quercus rubra...............	.588	.118	4.446	5.361	22.708	13.205	31.742	18.684
Quercus velutina.............	.011	.105	....	.349	....	16.494	.011	16.948
Betula lenta.................	.442	.005	4.969	....	10.504	....	15.915	.005
Cornus florida...............	.916	6.148	1.141	1.703	....	....	2.057	7.851
Liriodendron tulipifera.......	.069	....	.491	....	5.806	....	6.366	....
Carya tomentosa.............	....	.150	....	3.019	....	.863	....	4.035
Fraxinus americana..........	.135	.169	.315	.867	1.850	....	2.300	1.036
Quercus alba................	....	....	....	.190	....	1.755	....	1.945
Acer saccharum.............	.054	.019	1.276	.544	....	....	1.330	.563
Tilia americana.............	.305	.049	.546	....	.908	....	1.759	.049
Carya glabra................	.011	.272	.110	.632	.579	....	.700	.904
Acer rubrum................	.552	.109	.718	.183	....	....	1.270	.292
Fagus grandifolia............	.349	.127	.886	....	....	....	1.235	.127
Carya ovata.................	.008	.145	....	.462	....	....	.008	.607
Sassafras albidum............	....	.400	.196	....	....	....	.196	.400
Hamamelis virginiana........	.354	....	....	....	....	....	.354	....
Amelanchier arborea.........	.164	.021	.101	....	....	....	.265	.021
Ostrya virginiana............	.122	....	.120	....	....	....	.242	....
Ulmus rubra.................	....	.108	....	....	....	....	....	.108
Populus grandidentata........	....	.087	....	....	....	....	....	.087
Castanea aentata............	.041	....	....	....	....	....	.041	....
Morus rubra.................	....	.008	....	....	....	....	....	.008
Celtis occidentalis...........	....	.006	....	....	....	....	....	.006
	3.948	8.051	22.370	17.941	62.498	46.337	93.662	72.369

TABLE 8. Density per 3500 sq/m and frequency of trees on the north slope by size classes. The density figures for the size classes under 1 in. d.b.h. have been multiplied by proper factors to compensate for smaller quadrats used.

Name of Species	Indiv. Under 1 in. d.b.h.				Indiv. Over 1 in. d.b.h.						Total Density
	1 ft. tall or less		1 ft. tall or more		1.0 to 3.9 in.		4.0 to 9.9 in.		10 in. and over		
	D*	F	D*	F	D	F	D	F	D	F	
Fraxinus americana.........	3,500	69	1,738	97	5	9	1	3	2	6	5,246
Hamamelis virginiana.......	925	43	700	43	30	40	..	..	..	..	1,655
Betula lenta................	1,198	60	38	11	14	29	18	46	12	23	1,280
Acer rubrum................	750	31	306	34	32	40	5	11	..	..	1,093
Cornus florida..............	575	31	425	43	40	46	8	20	..	..	1,048
Quercus rubra...............	600	46	294	60	23	43	15	37	16	34	948
Liriodendron tulipifera.......	775	66	25	9	2	6	2	6	4	11	808
Quercus prinus..............	325	26	325	46	5	11	24	49	24	46	703
Sassafras albidum...........	375	29	325	20	..	..	1	3	..	..	701
Tilia americana.............	275	23	269	57	14	23	3	6	1	3	562
Quercus velutina............	125	14	169	20	2	6	..	..	..	..	296
Carya cordiformis...........	150	17	112	29	..	..	..	..	..	..	262
Carya glabra................	175	14	75	29	2	6	1	3	..	..	253
Prunus serotina.............	150	14	100	37	1	3	..	..	..	..	251
Ulmus rubra................	175	20	56	17	..	..	..	..	..	..	231
Ostrya virginiana...........	25	3	94	6	8	11	1	3	..	..	128
Castanea dentata............	..	..	69	11	3	9	..	..	..	..	72
Amelanchier arborea.........	..	..	62	14	8	11	1	3	..	..	71
Carya tomentosa.............	25	3	25	11	..	..	..	..	..	..	50
Carya ovata.................	25	6	12	6	1	3	..	..	..	..	38
Fagus grandifolia............	..	..	19	3	7	14	6	9	..	..	32
Celtis occidentalis...........	..	..	12	6	..	..	..	..	..	..	12
Acer saccharum.............	..	..	..	..	2	6	5	9	..	..	7
Nyssa sylvatica.............	..	..	6	3	..	..	..	..	..	..	6
Prunus avium...............	..	..	6	3	..	..	..	..	..	..	6
	10,148	..	5,262	..	199	..	91	..	59	..	15,759

TABLE 9. Density per 3500 sq/m and frequency of trees on the south slope by size classes. The density figures for the size classes under 1 in. d.b.h. have been multiplied by proper factors to compensate for smaller quadrats used.

Name of Species	INDIV. UNDER 1 IN. d.b.h.				INDIV. OVER 1 IN. d.b.h.						Total Density
	1 ft. tall or less		1 ft. tall or more		1.0 to 3.9 in.		4.0 to 9.9 in.		10 in. and over		
	D*	F	D*	F	D	F	D	F	D	F	
Cornus florida	4,400	86	3,800	94	330	100	19	37	..	..	8,549
Fraxinus americana	1,150	60	1,875	94	7	20	3	9	..	..	3,035
Sassafras albidum	1,725	60	638	63	21	17	..	..	..	..	2,384
Liriodendron tulipifera	1,925	51	69	23	..	..	..	..	..	..	1,994
Ulmus rubra	225	20	494	63	8	14	..	..	..	..	727
Quercus rubra	200	17	475	57	9	14	15	29	13	29	712
Quercus prinus	325	26	325	49	1	3	15	26	16	29	682
Quercus velutina	325	26	319	54	3	9	1	3	15	37	663
Betula lenta	625	31	25	9	1	3	..	..	..	..	651
Celtis occidentalis	100	11	475	40	1	3	..	..	..	..	576
Prunus serotina	325	6	75	20	..	..	..	..	..	..	400
Carya tomentosa	175	17	181	37	2	3	11	20	1	3	370
Carya cordiformis	225	26	106	23	..	..	..	..	..	..	331
Acer rubrum	200	17	69	20	6	11	1	3	..	..	276
Carya glabra	100	11	88	29	5	11	4	6	1	3	198
Tilia americana	25	3	75	20	1	3	..	..	..	..	101
Fagus grandifolia	50	3	38	11	10	9	..	..	..	..	98
Amelanchier arborea	50	6	19	9	2	6	..	..	..	..	71
Morus rubra	50	6	..	..	1	3	..	..	..	..	51
Acer saccharum	..	..	31	11	2	3	2	3	..	..	35
Quercus alba	..	..	25	9	..	..	1	3	2	6	28
Nyssa sylvatica	..	..	25	6	..	..	..	..	..	..	25
Castanea dentata	..	..	12	6	..	..	..	..	..	..	12
Fraxinus pennsylvanica	..	..	6	3	..	..	..	..	..	..	6
Ostrya virginiana	..	..	6	3	..	..	..	..	..	..	6
Carya ovata	..	..	..	..	3	9	1	3	..	..	4
Populus grandidentata	..	..	..	..	2	3	..	..	..	..	2
	12,200	..	9,251	..	415	..	73	..	48	..	21,987

Some idea of the difference in relative dominance among the species on the two slopes can be seen from the basal area figures in Table 7. The ten most important tree species on the north slope in order of decreasing total basal area are: *Quercus rubra* with approximately 34%, *Q. prinus* 30%, *Betula lenta* 17%, *Liriodendron tulipifera* 7%, *Fraxinus americana* 2.5%, *Cornus florida* 2%, *Tilia americana* 1.9%, *Acer saccharum* 1.4%, *Acer rubrum* 1.4%, and *Fagus grandifolia* 1.3%. On the south slope, the order is: *Quercus prinus* 26%, *Q. rubra* 26%, *Q. velutina* 23%, *Cornus florida* 11%, *Carya tomentosa* 5.6%, *Quercus alba* 2.7%, *Fraxinus americana* 1.4%, *Carya glabra* 1.2%, *C. ovata* 0.8%, and *Acer saccharum* 0.7%.

Although *Cornus florida* was included in the list of tree canopy species, it actually belongs to a lower layer. This species is much more important on the south slope where it forms an almost continuous layer under the main tree canopy. On the north slope, *Hamamelis virginiana* makes up the greater part of this layer but the individuals do not reach tree size so frequently nor is the layer so continuous. In terms of total basal area, *H. virginiana* has twelfth place with only 0.4% on the north slope and did not occur in the quadrats on the south slope.

The total density or number of individuals in all size classes of each tree species shows still further differences in the vegetation of the two slopes. In comparing total densities, individuals of all size classes (hence the reproductive potential) are included (Tables 8 & 9). These totals, however, obscure the survival tendencies which can only be obtained by reference to all five size classes for each species. From the total density values it can be seen that the species present in the largest numbers are not the same as those contributing the greatest total basal area. On the north slope the ten most abundant species in order of decreasing total density are: *Fraxinus americana, Hamamelis virginiana, Betula lenta, Acer rubrum, Cornus florida, Quercus rubra, Liriodendron tulipifera, Quercus prinus, Sassafras albidum* and *Tilia americana*. For the south slope, the first ten in order of decreasing total density are: *Cornus florida, Fraxinus americana, Sassafras albidum, Liriodendron tulipifera, Ulmus rubra, Quercus rubra, Q. prinus, Q. velutina, Betula lenta,* and *Celtis occidentalis*. Seven species rank among the ten most abundant on both slopes. Only four of these seven rank among the ten species with highest total basal area on both slopes.

TABLE 10. Density per 560 sq/m and frequency for the shrub species on the two slopes. The data for the individuals under 1 ft. in height have been multiplied by the proper factor to compensate for smaller quadrats used.

Species	North Slope					South Slope				
	Under 1 ft.		Over 1 ft.		Total	Under 1 ft.		Over 1 ft.		Total
	D*	F	D	F	D	D*	F	D	F	D
Viburnum acerifolium.........	942	97	1,844	100	2,786	536	77	744	77	1,280
Parthenocissus quinquefolia.....	2,744	97	203	66	2,947	264	57	27	17	291
Cornus florida...............	92	31	68	43	160	704	86	608	94	1,312
Rhododendron nudiflorum......	344	26	207	23	551	..	..	..	..	..
Rhus radicans...............	196	34	19	20	215	120	29	29	11	149
Corylus cornuta..............	72	23	213	60	285	4	3	15	6	19
Hamamelis virginiana.........	148	43	112	43	260	..	..	..	..	..
Prunus virginiana............	40	3	150	31	190	..	..	1	3	1
Vaccinium angustifolium.......	44	24	108	31	152	12	9	23	6	35
Gaylussacia baccata...........	56	17	105	9	161	..	..	..	..	..
Vitis aestivalis...............	4	3	5	11	9	104	49	34	26	138
Rubus flagellaris.............	..	..	2	3	2	76	17	..	..	76
Celastrus scandens...........	20	14	19	20	39	28	14	8	14	36
Rosa carolina...............	4	3	..	..	4	32	6	25	9	57
Clematis verticillaris..........	36	17	12	11	48	..	..	..	..	..
Ceanothus americanus........	..	..	..	..	..	44	14	3	9	47
Cornus alternifolia...........	12	6	21	17	33	..	..	3	6	3
Rubus occidentalis...........	8	6	..	..	8	16	9	9	17	25
Vaccinium vacillans..........	8	3	1	3	9	20	6	3	6	23
Rubus frondosus.............	..	..	..	..	..	8	3	24	3	32
Viburnum prunifolium........	..	..	..	..	..	8	6	20	17	28
Diervilla lonicera.............	4	3	21	3	25	..	..	..	..	..
Lonicera japonica............	..	..	..	..	..	24	9	..	..	24
Rubus odoratus..............	12	9	10	6	22	..	..	..	..	..
Lindera benzoin..............	..	..	7	17	7	4	3	..	..	4
Cornus racemosa.............	..	..	..	..	..	..	..	10	6	10
Cornus rugosa...............	..	..	4	6	4	4	3	..	..	4
Vaccinium stamineum.........	4	3	..	..	4	..	..	2	3	2
Crataegus uniflora...........	..	..	..	..	..	..	..	3	6	3
Total density of shrubs over 1 ft. high........	..	..	3,131	..	7,921	..	..	1,591	..	3,599

THE SHRUB LAYERS

Casual observation indicates the shrub vegetation of the two slopes to be quite different. This layer is more nearly continuous and has a more varied composition on the north slope. The total density values in Table 10 indicate that there are twice as many shrub stems on the north slope. On the south slope, not only is the layer discontinuous, it is quite variable in height due to the presence on that slope of many individuals of *Cornus florida* under one inch d.b.h.

The most abundant species in the shrub layer on both slopes is *Viburnum acerifolium*. The degree to which this species dominates the shrub layer is not the same on both slopes, however. On the north slope it contributes almost 60% of the total shrub density, while on the south slope it accounts for only 47%. This species and individuals of *Cornus florida* under 1 in. d.b.h. make up 85% of the total shrub density of the south slope. On the north slope, in addition to *Viburnum acerifolium*, there are seven species each of which contribute over 2% to the total shrub density. On the south slope, in addition to this species, only *Cornus florida* contributes over 2%.

The relative importance of the shrub species is different between the slopes. On the north slope, the ten species with the highest total density of stems over one foot high are, in order of decreasing density: *Viburnum acerifolium, Corylus cornuta, Rhododendron nudiflorum, Parthenocissus quinquefolia, Prunus virginiana, Hamamelis virginiana, Vaccinium augustifolium, Gaylussacia baccata, Cornus florida,* and *C. alternifolia*. On the south slope, the first ten are: *Viburnum acerifolium, Cornus florida, Vitis aestivalis, Rhus radicans, Parthenocissus quinquefolia, Rosa carolina, Rubus frondosus, Vaccinium angustifolium, Viburnum prunifolium,* and *Corylus cornuta*. When the species are listed in order of decreasing density based upon the sum of the values for stems over and under one foot in height, some shifting in sequence occurs. This is due both to the amount of reproduction and to the growth form of the species. For example, *Parthenocissus quinquefolia* has a high density of stems under one foot in height due to its sprawling over the ground and the presence of many short upright stems. When ranked on the basis of all stems, including the short ones under one foot in height, this species takes first place on the north slope and second place on the south slope. Since these very short stems of Parthenocissus and other shrub species produce leaves which in reality function in the herbaceous layer, it seems best to consider only woody stems over one foot in height as belonging to the shrub layer.

Shrub reproduction, both from seedlings and from

root sprouts is plentiful for most of the species. The data in Table 10 for stems under one foot in height give an idea of the relative amounts of reproduction for many species. The figures for *Parthenocissus quinquefolia* as mentioned above do not represent reproduction. This is true in part for *Rhus radicans* but not to the same degree as the former species.

THE HERB LAYERS

The differences in herbaceous vegetation between the two slopes are somewhat more marked than the differences in the two higher layers. In contrast with

TABLE 11. Density per 140 sq/m and frequency of the herbaceous species on the north slope. The frequency value is the percent of the 35 groups of 4 quadrats in which the species occurred.

Species	D	F
Aster divaricatus	514	100
Asarum canadense	372	63
Aralia nudicaulis	330	77
Solidago caesia	206	86
Polygonatum pubescens	118	80
Galium triflorum	96	66
Polypodium virginianum	95	26
Cimicifuga racemosa	83	66
Collinsonia canadensis	79	57
Amphicarpa bracteata	72	51
Dryopteris marginalis	71	80
Viola pubescens	56	49
Arisaema triphyllum	53	54
Mitchella repens	50	23
Desmodium nudiflorum	48	49
Anemonella thalictroides	44	17
Galium circaezans	37	40
Smilacina racemosa	33	46
Viola septentrionalis	33	17
Aquilegia canadensis	27	23
Desmodium glutinosum	25	23
Carex virescens	22	26
Uvularia perfoliata	15	14
Festuca obtusa	15	11
Adiantum pedatum	13	9
Carex radiata	12	20
Hepatica americana	12	14
Circaea quadrisulcata var. *canadensis*	10	11
Carex pensylvanica	9	9
Sanguinaria canadensis	8	14
Sphenopholis nitida	8	6
Prenanthes altissima	5	11
Aster infirmus	5	6
Heuchera americana	5	3
Polygonatum canaliculatum	4	9
Geranium maculatum	4	3
Carex digitalis	3	9
Botrychium virginianum	3	9
Galium lanceolatum	3	6
Agrostis hyemalis	3	6
Dryopteris noveboracensis	3	3
Polystichum acrostichoides	3	3
Smilax herbacea	2	6
Sanicula marilandica	2	6
Lysimachia quadrifolia	2	3
Melanthium hybridum	2	3
Agrimonia rostellata	1	3
Lespedeza violacea	1	3
Hieracium paniculatum	1	3
Dioscorea villosa	1	3
Carex platyphylla	1	3
Potentilla canadensis	1	3
Gerardia flava	1	3

the shrub layers, the most highly developed herbaceous vegetation exists on the south slope. Both in terms of numbers of abundant species and density of individuals, the south slope has first place.

The herbaceous species with the highest total density on both slopes is *Aster divaricatus*. In addition to this species, several others such as *Solidago caesia* and *Amphicarpa bracteata* are among the most abundant on both slopes. The herbaceous species encountered in the herb quadrats on both slopes are listed in order of decreasing total densities in Tables 11 & 12. From these data, it can be seen that except for a few species, as indicated above, the herb layers are quite different. Several species such as *Asarum canadense*, *Aralia nudicaulis*, *Cimicifuga racemosa*, *Collinsonia canadensis*, and *Aquilegia canadensis* which are important members of the north slope herb layer were either absent from the south slope quadrats or, as in the case of *Cimicifuga racemosa*, fairly uncommon. Among the species found to be much more common on the south slope are: *Cunila origanoides*, *Viola palmata*, *Lespedeza violacea* and *Eupatorium sessilifolium*.

Grasses, sedges and annuals are more important on the south slope. The ferns, however, are more important on the north slope. Among the grasses and sedges which are more common to the south slope are *Muhlenbergia sobolifera*, *Panicum boscii*, *Carex pensylvanica* and *Hystrix patula*. Some of the annuals more common to this slope include *Hedeoma pulegioides*, *Paronychia canadensis*, *Specularia perfoliata*, *Polygonum convolvulus*, *Cardamine parviflora*, *Cerastium nutans*, and *Cassia nictitans*. Most of the ferns encountered in the study are much more common on the north slope. *Asplenium platyneuron*, however, is much more common to the south slope. *Botrychium virginianum* is occasional on both slopes.

The herbaceous layers on the two slopes are not homogeneous over the area studied. Minor variations occur from place to place and rather marked variations occur where small openings exist in the tree and shrub canopies. In the larger of these openings (2–5 m in diam.) the greatest differences occur. On the south slope, the herb layer in these places takes on a marked "grassy" appearance. In such areas, grasses, sedges, *Lespedeza violacea*, *Desmodium paniculatum*, *Solidago nemoralis*, annuals and many tree and shrub seedlings occur. Such areas on the north slope may be occupied by ferns, sedges, *Aralia nudicaulis*, *Circaea quadrisulcata* var. *canadensis*, *Cimicifuga racemosa*, and many tree and shrub seedlings. However, more often on the north slope, such areas are occupied by shrubs. Under more continuous canopy on the two slopes species such as *Aster divaricatus*, *Galium circaezans*, *Polygonatum pubescens*, *Amphicarpa bracteata*, and *Smilacina racemosa* occur.

THE BRYOPHYTE LAYER

The bryophytic vegetation on the ridge can be described as a discontinuous layer made up of a mosaic of many different groups of species. This layer may occur on soil, rock, rotted wood, tree trunk bases, and even well up the trunks of the trees as

TABLE 12. Density per 140 sq/m and frequency of the herbaceous species on the south slope. The frequency value is the percent of the 35 groups of 4 quadrats in which the species occurred.

Species	D	F
Aster divaricatus	1466	100
Solidago caesia	1008	100
Muhlenbergia sobolifera	503	69
Galium circaezans	317	80
Amphicarpa bracteata	267	91
Smilacina racemosa	209	77
Panicum boscii	178	66
Carex pensylvanica	175	71
Desmodium nudiflorum	163	69
Hedeoma pulegioides	143	46
Paronychia canadensis	126	49
Hystrix patula	116	40
Carex radiata	91	60
Festuca obtusa	91	29
Specularia perfoliata	75	31
Polygonum convolvulus	73	46
Cunila origanoides	69	37
Galium triflorum	63	34
Saxifraga virginiensis	59	23
Carex virescens	53	54
Viola palmata	39	43
Sphenopholis nitida	32	31
Eupatorium sessilifolium	32	29
Agrostis hyemalis	32	14
Danthonia spicata	30	9
Uvularia perfoliata	28	29
Potentilla canadensis	27	17
Cardamine parviflora	27	9
Polygonatum pubescens	26	34
Lespedeza violacea	24	20
Cerastium nutans	24	9
Cassia nictitans	23	11
Polygonatum canaliculatum	21	34
Galium lanceolatum	18	11
Desmodium paniculatum	16	20
Viola pubescens	14	14
Carex platyphylla	14	14
Aster lowrieanus	13	17
Aster infirmus	12	14
Eupatorium rugosum	12	11
Phytolacca americana	11	20
Carex cephalophora	11	14
Chimaphila maculata	10	14
Circaea quadrisulcata var. canadensis	10	6
Silene stellata	9	14
Helianthus divaricatus	9	14
Arisaema triphyllum	8	7
Asplenium platyneuron	7	11
Oxalis stricta	7	9
Desmodium rotundifolium	7	6
Aster anomalus	6	11
Aster lateriflorus	6	9
Agrimonia pubescens	5	14
Antennaria plantaginifolia	5	6
Hepatica americana	4	9
Teucrium canadense	4	6
Geum virginianum	4	3
Geranium maculatum	3	9
Carex digitalis	3	9
Erigeron pulchellus	3	6
Dioscorea villosa	3	3
Liparis lilifolia	2	6
Cimicifuga racemosa	2	6
Botrychium virginianum	2	6
Aristolochia serpentaria	2	6
Hackelia virginiana	2	6
Hieracium paniculatum	2	3
Desmodium glutinosum	1	3
Carex muhlenbergii	1	3
Dryopteris marginalis	1	3
Fragaria virginiana	1	3

Species	D	F
Sanicula marilandica	1	3
Poa pratensis	1	3
Thalictrum dioicum	1	3
Orobanche uniflora	1	3
Menispermum canadense	1	3

well as in deep crevices between the rocks. The differences in this layer of vegetation between the two slopes are greater than in any of the other layers.

As might be expected, the terrestrial bryophyte layer is much better developed on the north slope. On the basis of the sampling, the cover of this layer is almost twenty-five times greater on the north than on the south slope (Table 13). The average frequency of bryophytes is also considerably greater on the north slope, the value being 16.9% as opposed to 1.8% for the south slope. Three species were encountered in the quadrats on both the north and the south slopes. Two of these, *Eurhynchium serrulatum* and *Sematophyllum carolinianum* var. *admixtum* were the most important mosses on both slopes. This greater importance of one or two species on both slopes corresponds to a similar situation in the other three layers.

Eleven species in addition to the two mentioned above were encountered in the quadrats on the north

TABLE 13. Frequency and cover values for the terrestrial bryophytes on the north and south slopes. The data are based upon 100 1/10 sq/m quadrats for the south slope and 50 such quadrats for the north slope.

Species	NORTH SLOPE		SOUTH SLOPE	
	F	Average percent cover	F	Average percent cover
Eurhynchium serrulatum	60	1.4	7	0.15
Sematophyllum carolinianum var. admixtum	46	2.0	2	0.09
Lophocolea heterophylla	52	2.4		
Dicranum fuscescens	30	1.0		
Mnium cuspidatum	12	0.6		
Campylium chrysophyllum	12	0.1		
Dicranum fulvum	6	1.5		
Fissidens osmundioides	6	0.04		
Amblystegium serpens	2	0.2	1	0.001
Brachythecium scalebrosum	2	0.2		
Brachythecium oxycladon	2	0.2		
Entodon seductrix	2	0.04		
Anomodon attenuatus	2	T		
Thuidium virginianum	..	...	2	0.05
Dicranella heteromalla var. orthocarpa	..	...	1	0.05
Sematophyllum adnatum	..	...	1	0.03
Campylium hispidulum	..	...	2	0.03
Physcomitrium turbinatum	..	...	1	0.015
Pohlia nutans	..	...	1	0.015
Homomallium adnatum	..	...	1	0.01
Grimmia pilifera	..	...	2	0.002
Bryum capillare	..	...	1	0.001
Atrichum macmillani	..	...	1	0.001
Average frequency and total cover	16.9	9.7	1.8	0.4

slope. These species are listed in Table 13 in decreasing order of importance as indicated by the frequency and cover values. The more common terrestrial species occurring on the north slope but not encountered in the quadrats are listed below in decreasing order of importance: *Atrichum macmillani, Plagiothecium denticulatum, Thidium delicatulum, Ptilidium pulcherrimum, Aulacomnium heterostichum, Dicranum scoparium, Eurhynchium hians, Leucobryum glaucum, Entodon cladorrhizans, Bazzania trilobata, Jamesoniella autumnalis, Porella platyphylloidea, Bartramia pomiformis, Cirriphyllum boscii, Pohlia nutans, Mnium affine, M. stellare,* and *Diphysicum foliosum.*

On the south slope, in addition to those encountered in the quadrats, the following are the more important terrestrial species: *Ditrichum pallidum, Tortella humilis, Weisia viridula, Hedwigia ciliata, Ptychomitrium incurvum, Mnium cuspidatum, Anomodon attenuatus, Ceratodon purpureus, Thuidium microphyllum,* and *Porella platyphylla.*

The corticolous bryophyte vegetation layer of the ridge is, for the most part, made up of different species that make up the terrestrial layer. The best development of this layer occurs on the lowest 50 cm of the tree trunks although a few species occur at greater heights. A larger number of the trees on the north slope support colonies of this layer than on the south slope. Few trees are totally devoid of bryophytes, but well developed colonies are present on less than 25% of the trees on the north slope and on less than 10% of the trees on the south slope.

Contrary to the situation in the terrestrial bryophytic layer and all the higher layers of vegetation, the most important corticolous species are not the same on both slopes (Table 14). In addition to the

TABLE 14. Frequency values and presence for corticolous bryophytes on the north and south slopes. The frequency data are based upon a sample of 8 trees on the north slope and 18 trees on the south slope.

Species	NORTH SLOPE		SOUTH SLOPE	
	% F	P	% F	P
Sematophyllum carolinianum var. *admixtum*............	..	x	28	x
Frullania eboracensis.........	..	..	22	x
Sematophyllum adnatum.....	..	x	17	x
Thelia asprella.............	..	x	17	x
Porella platyphylloidea......	..	x	12	x
Platygyrum repens..........	12	x	11	x
Homomallium adnatum.......	..	x	11	x
Orthotrichum strangulatum...	..	..	11	x
Amblystegiella subtilis.......	..	x	6	x
Heterophyllium haldanianum.	..	x	6	x
Leskea gracilescens..........	..	x	6	x
Thelia hirtella..............	..	..	6	x
Dicranum fuscescens........	75	x	6	x
Lophocolea heterophylla......	50	x	6	x
Lophocolea bidentata.........	25	x		
Ptilidium pulcherrimum......	12	x		
Plagiothecium denticulatum...	12	x		
Schwetschkeopsis denticulata..	12	x		
Eurhynchium serrulatum.....	12	x		
Cephalozoia bicuspidata..	12	x		

species encountered in sampling, *Amblystegium serpens* and *Campylium hispidulum* were collected from trees on the north slope, and *Amblystegium serpens, Entodon seductrix, Fissidens subbasilaris, Leskea polycarpa, Campylium hispidulum,* and *Thelia hirtella,* were collected from trees on the south slope.

PERIODICITY OF THE COMMUNITIES ON THE TWO SLOPES

"Sociological periodicity depends upon the beginning, the duration, and the seasonal course of the struggle for existence" (Braun-Blanquet 1932). Periodicity includes the time of shoot elongation, duration of foliage, leaf fall and root development as well as flowering, fruiting and other events. A study of the differences in the general periodicity of plant communities is an excellent method of comparing the vegetation of two areas. Differences between the periodicity of individuals of the same species are often used in comparing habitats (Hopkins & Murray 1932; Huberman 1941).

In the present study, dates of first elongation of vegetative stems, first flowering, leaf expansion, foliage coloration and leaf fall were observed in many species growing on the two slopes. Observations were also made of the diameter increase of a few trees on each slope. Although the study of periodicity of the two communities is by no means complete, certain data were obtained which show the different characters of the two plant communities.

The most obvious differences in the periodicity of the vegetation on the two slope exposures are apparent during the transition from winter to spring. This change in seasons, marked by the breaking of dormancy in the buds and stems near the surface (Wolfe *et al.* 1949), occurs from two to three weeks earlier on the south slope. Such events as the first elongation of *Potentilla canadensis,* the elongation of the flower stalks of *Hepatica americana* and other activity were observed during the first week of March in 1949 and during the second week of March in 1950 on the south slope. The same degree of activity in these species occurred on the north slope two weeks later in both years.

In general, the time of breaking of dormancy occurs later in the upper layers of vegetation. As this event reaches greater heights, from the herb layer to the tree layer, the difference between the slopes in the time of occurrence in any one species decreases. The first flowering of *Lindera benzoin* and small individuals of *Acer rubrum* (under 2 m in height), occurred less than one week earlier on the south slope. No difference was observable in the time of breaking of dormancy in any of the upper tree canopy species.

The vernal season on the two slopes, extending from the breaking of dormancy until the closing of vegetative canopy (Braun-Blanquet 1932, Wolfe *et al.* 1949), brings out further differences in the periodicity of the two plant communities. On the south slope, most of the annuals make their most rapid growth at this season. *Cerastium nutans* and *Cardamine parviflora* have almost completed their life cycles before the canopy closes. On the north slope,

annuals are essentially absent. However, the perennial *Anemonella thalictroides*, primarily a north slope species, has completed much of its annual cycle by the time of the closing of the canopy. Also, the north slope is characterized by having a greater abundance of species which first flower before the closing of the canopy than has the south slope. Of the ten most abundant flowering herbs on the north slope, five begin blooming before canopy closure. These are *Asarum canadense, Aralia nudicaulis, Polygonatum pubescens, Galium triflorum* and *Viola pubescens*. Of the ten most abundant flowering herbs on the south slope, only *Carex pensylvanica* and *Smilacina racemosa* bloom before the end of the vernal season.

The aestival season began during the second week of May in 1948 and in the first week in 1949. The tree canopy is closed a few days earlier on the north slope than on the south slope. This is due to the presence on the former slope of large numbers of *Betula lenta*, a species which expands its foliage at a slightly greater rate than the oaks and hickories that characterize the latter slope. The beginning of the aestival season corresponds with the peak of the grand period of growth for the vegetation of the two slopes. The leaves on almost all species are growing rapidly and many species are flowering.

In both 1948 and 1949, a biotic phenomenon occurred that is opposite in effect to the closing of the tree canopy. This was the almost complete defoliation of several of the important tree species by the spring canker worm, *Paleacrita vernata* Peck. This insect, and possibly others, removed almost all of the photosynthetic tissue from *Tilia americana* and *Quercus prinus*. Other trees were attacked in varying degrees of severity. In general, the effect on the north slope was more severe than on the south. This was due to a greater abundance there of the hard-hit species, and a slightly greater degree of damage per tree for many species.

It is of interest to know something of the periodicity and relative amount of growth produced during the aestical season by the plant communities on the two slopes. Quantitative observations were not made of growth in either the shrub or herb layers but, measurements were made of changes in the radial dimensions of three oaks on each slope. These measurements were made with the Daubenmire (1945) dendrometer during the growing season of 1949. Measurements were made on both the east and north side of each tree. Two of the trees measured on each slope were individuals of *Quercus rubra*. The third tree was *Q. prinus* on the north slope and *Q. velutina* on the south slope. All three species show the same trends for the same periods. Changes in radii as indicated by dendrometer measurements are a combination of vascular cambium activity and changes in water content of xylem, phloem and periderm tissue (Lodewick 1923; Byram & Doolittle 1950). Phellogen activity may also account for small changes. From Figs. 3 and 4 it can be seen that the trees on the south slope increased in radius more
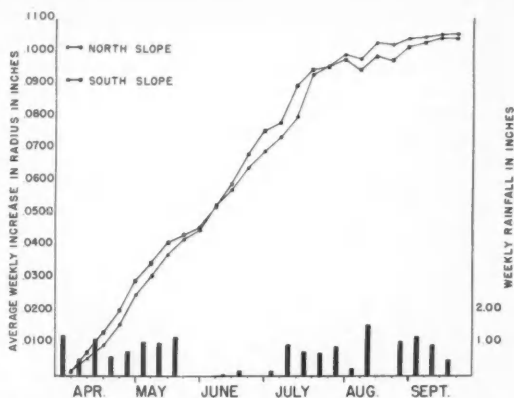

FIG. 3. The increase in radius of three oaks on each slope for 1949 growing season together with weekly rainfall. Note crossing of the curves during the last week of July.
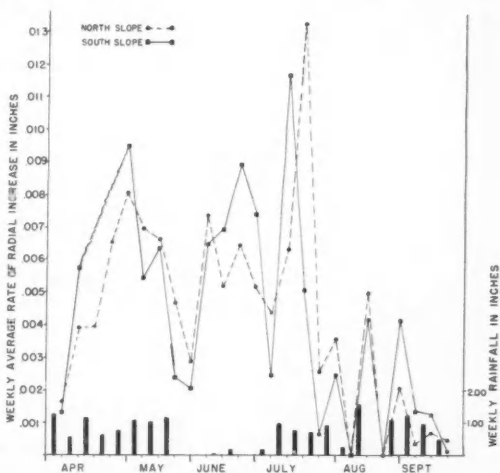

FIG. 4. Weekly rate of increase in radius for three oaks on each slope for 1949 growing season together with weekly rainfall. The wavy line connecting the second and fourth weeks of April indicates lack of points for that period on the south slope. The zero rates indicated for the first and third weeks of August are actually negative rates, the trees becoming smaller in radial dimensions during these weeks.

rapidly during the early part of the growing season. By the end of the growing season, however, the trees on the north slope had made the largest increases.

The curves for the radii changes of the trees on both slopes seem to show a marked response to the rather severe drought which characterized much of the 1949 growing season. This can be seen in Fig. 3 where the average increase in radius for the three trees on each slope is plotted together with the weekly rainfall. The rainfall data are from Clinton, New Jersey, 4 mi. west of the area studied. The trees on the south slope seem to show a more marked response to the rainless periods than the trees on

the north slope. During the dry period in late May and June, the average increase in radius of trees on the south slope gradually decreased until on June 10 it fell behind that for the north slope trees. With the very light rains which occurred during the third and fourth weeks of June, the south slope trees again made larger radial increases. During the latter part of the growing season, the radial increase of the trees on the north slope again exceeded that of the trees on the south slope.

The rates of radial increase (Fig. 4) also may show a relationship to precipitation. During the June drought, the rate of radial increase fell more sharply on the south slope. That the rate of radial increase is not entirely a matter of precipitation however, is shown by the sharp decline during the wet period in May demonstrated by all species and reflected in the averages presented. This decline may be associated with the natural cycle of the species involved. It occurs in mid-May when the leaves of these oaks are almost completely expanded. The rise and fall in radius indicated in the figures during the latter part of the growing season are probably due to changes in water content of the tissues (Byram & Doolittle 1950).

In addition to the difference in the summer changes in tree trunk radii, further differences between the slopes in vegetation periodicity become apparent at this season. The number of herbaceous species which bloom in the late summer is much greater on the south slope. These include, among others, *Lespedeza* spp., *Desmodium* spp., *Cunila origanoides*, *Solidago* spp., *Aster* spp. and several grasses. In 1949, the summer drought caused some leaf fall in individuals of several species on both slopes, especially in the less favorable sites. Of the drought affected species, the individuals on the south slope suffered the most, some failing to recover following the rains of July and August.

The change in seasons from summer to fall is characterized by the beginning of coloration in the vegetation. The time of this change is somewhat more difficult to fix than the closing of the canopy. Drought induced coloration and leaf fall may occur considerably earlier than the true annual change in seasons. Generally speaking, if the time of appearance of color in the individuals in average habitats, rather than in the more xeric habitats, is used, the date may be fixed more definitely.

No difference was observed between the slopes in the date of change in seasons from summer to fall. In 1948, autumn coloration appeared in the third week in September while in 1949, it appeared during the second week. Although coloration appeared at the same time on both slopes, the height of color was not the same on the two slopes in all species. *Viburnum acerifolium* seems to show much deeper color on the north slope, the individuals having more purple; while those on the south slope are more nearly red in color. *Cornus florida* appears brighter on the south slope, the individuals on the north slope appearing dull in comparison.

The herb layer on the north slope develops color and thins out more rapidly than that on the south slope. This contrast in aspect is due to the difference in dominant species in this layer on the two slopes. The foliage of *Aralia nudicaulis*, *Cimicifuga racemosa*, several species of ferns and other plants declines rapidly on the north slope. On the south slope, *Aster* spp., *Solidago* spp., *Desmodium* spp., *Lespedeza* spp., the grasses and sedges and many other species remain green for a much longer period.

Many more species remain in flower on the south slope during this period than on the north slope. The only woody species which first flowers at this season, however, is *Hamamelis virginiana*, a north slope species. Several species of herbs flower for the first time with the coming of fall; two are predominantly north slope species, *Collinsonia canadensis* and *Prenanthes altissima*; the rest are more abundant on the south slope. These include *Cassia nictitans*, *Solidago nemoralis*, *Cunila origanoides*, *Lespedeza hirta*, *Aster patens*, *A. anomalus* and others.

Coloration, leaf fall, and death of foliage progresses at an increasing rate until the communities are nearly devoid of photosynthetic tissue. In general, the rate is more rapid on the north slope due to the more rapid deterioration of the herb layer and to the abundance of woody species which lose their leaves early. *Betula lenta*, *Corylus cornuta*, *Hamamelis virginiana*, and *Prunus virginiana*, all abundant on the north slope, lose their foliage early. The oaks in general, and particularly *Quercus velutina* and *Q. rubra*, retain their leaves longer. In 1949 the latter species retained green leaves a full two weeks longer than all other native tree species. *Fagus grandifolia*, present on both slopes, may retain many of its dead leaves throughout the winter. The few individuals of *Acer platanoides*, present on both slopes, were very late in showing coloration and leaf fall.

The vegetation on both slopes was practically devoid of leaves by the second week of November in 1948 and by the third week in 1949. This event has been suggested by Hopkins & Murray (1932) and Wolfe *et al.* (1949) among others, as the beginning of winter. The winter season brings out still further differences in periodicity between the slopes. The herbaceous seed plants with winter rosettes are more abundant on the south slope, while the ferns and bryophytes which remain green throughout the year are more abundant on the north slope.

During the warmer periods in winter the grasses, sedges and some of the rosette plants can be observed to produce new leaves or make leaf growth on the south slope. In the two winters in which observations were made only one such warm period resulted in noticeable greenness in the grasses, sedges and rosette plants on the north slope (the last week in December 1949).

Two of the annuals which occur exclusively on the south slope germinate and produce several nodes during the winter. These are *Cerastium nutans* and

Cardamine parviflora. These species germinate during December and January and by the time perennial species begin to break dormancy, they have produced several nodes. No species of winter annuals occur on the north slope.

Several of the perennial plants such as *Galium triflorum* and *Solidago caesia* which occur on both slopes produce many more leaves and longer stems on the south slope during the winter. These species and others that do not produce noticeable numbers of new leaves can be observed to increase and decrease in redness on the south slope as the weather alternates from cold to warm during the winter. Such alternation on the north slope is not frequent. During this season and early spring the differences in periodicity between the slopes are most noticeable.

DISCUSSION

DIFFERENCES IN THE MICROCLIMATIC STRUCTURE ON THE TWO SLOPES

The results of this study indicate that the microclimates and soil temperatures of north and south facing slopes are quite different. The air temperature, soil temperature and vapor pressure deficit are generally higher on the south slope. The magnitude of the differences in the microclimatic layer between the slopes increases toward the ground. This increasing difference toward the ground results from a different daytime microclimatic structure on the two slopes.

During the leaf season, the microclimatic layer on the south slope is characterized by three general daytime types. Under heavy shade, the air temperature may be slightly lower near the ground or forest floor than at greater heights. This condition is the same as has been described for forest microclimate by several investigators (Geiger 1950, Baum 1949a, Chapman *et al.* 1931). Under medium shade, the daytime temperature profile is generally isothermal with no great difference in air temperature with height. In small openings, which seem to be a natural feature in the tree layers, air temperature is much more variable with height, the higher daytime temperatures occurring near the ground. There may be as much as 13° F difference between the maximum air temperatures at 5 cm and at 2 m in such small openings. Areas characterized by such microclimatic structure are abundant on south slopes. The temperature profile in these areas is similar to that described by Geiger (1950) for clearings in forest vegetation on level ground.

During the leafless season, there is but one general daytime microclimatic type on the south slope. At this season, the air temperature is higher in the lower layers.

On the north slope, the microclimatic structure is entirely different. During the daytime, the air temperatures are characteristically lower near the ground through much of the year. This type of microclimatic structure prevails on the north slope under both heavy and light tree canopy shade. Only under

very large openings in the tree layer does the structure of the microclimate change materially.

This lower temperature near the ground results in a much greater difference in vapor pressure deficit between the 2-m and 5-cm level on the north slope. Byram (1948) states that on very steep north slopes the air temperatures may be low enough in the air spaces of the litter to cause condensation to occur. It would seem probable that these low temperatures and improved water relations are of considerable importance to the terrestrial bryophyte and herb layers.

DIFFERENCES IN COMPOSITION AND STRUCTURE OF THE TWO COMMUNITIES

Observation and quantitative analysis of the plant communities on the two slopes reveal them to be quite different. In general, the degree of difference in vegetation between the slopes increases toward the surface. This can be seen if the vegetation on the slopes is studied by layers. Such a study may be made by comparing, for each structural character, the sum of the differences between the slopes with the sum of the values for that character on the two slopes. For example, if species A has a frequency of 10% on the south slope and 40% on the north slope, the difference is 30. The sum of these differences in frequency between the slopes is then obtained for all the species in that particular layer. This sum is then divided by the sum of all the frequency values for all the species in that layer on both slopes. The quotient is then multiplied by 100 and the resulting product is called the degree of vegetation difference for the particular structural character. All species occurring in each layer are considered even though they may ultimately exist in another layer.

The calculation is as below:

$$\frac{\text{Sum of the differences in the character between the slopes for all species}}{\text{Sum of the values for the character on both slopes for all species}} \times 100 = \text{degree of vegetation difference}$$

Such calculations were made for the tree layers using the characters density and basal area, for the shrub and herb layers using density and frequency, and for the bryophyte layer using frequency and cover. In making the calculations for the upper tree layer, all those individuals over 4 in. d.b.h. were considered as contributing to that layer. The four inch separation was used since this separated out almost all of the sub-tree canopy species such as *Cornus florida.*

The results of these calculations show, in general, an increasing degree of vegetation difference between the slopes toward the surface (Table 15). The exception to this trend is the small tree layer which shows a much greater difference than either the tree or the shrub layer. This layer has an almost completely different composition on the two slopes. On the south slope, *Cornus florida* contributes over one

TABLE 15. The degree of vegetation difference between the slopes for the various layers. The value is obtained by dividing the sum of the differences in various characters (density, frequency, etc.) between the two slopes by the sum of the character for both slopes (see text).

Layer and the character used to obtain the degree of difference	Degree of difference between the slopes expressed in percent
Tree layer	
Density	45
Basal area	46
Lower tree layer	
Density	74
Basal area	75
Shrub layer	
Frequency	53
Density	40
Herb layer	
Frequency	52
Density	72
Bryophyte layer	
Frequency	92
Cover	95
Average difference	64

half of the basal area and over three fourths of the number of individuals to this layer. On the north slope, although *C. florida* is still the most abundant species, it contributes less than one fourth of the basal area and less than one fifth of the number of individuals. Reproduction of the upper tree canopy species make up a larger portion of this layer on the north slope (Tables 7, 8 and 9).

Although the differences in the upper tree layers of the two slopes are smaller than for any of the other layers, the degree of difference is still around 45%. The greatest differences are due to the absence of large individuals of *Betula lenta* from the south slope quadrats and of *Quercus velutina* from the north slope quadrats. Although both of these species occur in the larger size classes on the opposite slope, they are not common. On the north slope, *Betula lenta* contributes almost one fourth of the total density and basal area to this layer. Similarly, on the south slope, *Quercus velutina* contributes almost one fourth of these values. Further important differences in this layer are the contributions of *Liriodendron tulipifera* on the north slope and of *Carya tomentosa* on the south slope (Table 7). The larger number of trees over four inches d.b.h. and the greater total basal area on the north slope also add to the differences between the slopes in this layer of vegetation.

There is a slightly greater degree of difference between the shrub layers on the two slopes than between the upper tree layers. Much of this difference is due to the presence of shrub species in the quadrats of one slope in fairly high numbers and the absence of these species from the opposite slope.

Table 10 shows 12 shrub species which were not encountered in the quadrat samples on both slopes. Of this number, the following 5 species were not observed at any time on the opposite slope: *Rhododendron nudiflorum, Clematis verticillaris, Ceanothus americanus, Diervilla lonicera* and *Lonicera japonica*. The other 8 species were uncommon on the other slope.

The rather large differences between the slopes in the frequency and number of individuals of some species also add to the difference. For example, there are almost nine times as many individuals of *Cornus florida* in the shrub layer on the south slope, and over two and one half times as many individuals of *Viburnum acerifolium* on the north slope.

The contribution to the shrub layer by tree reproduction (over one foot high and under one inch d.b.h.) is not the same on the two slopes. From Tables 8 and 9, it can be seen that there are more individuals in this group on the south slope. If *Cornus florida* is omitted from consideration however, the total number of individuals is nearly the same on the two slopes. Individual tree species are not represented by the same abundance of reproduction on the two slopes, however. On the south slope, *Quercus velutina, Q. rubra, Q. alba, Carya tomentosa, Liriodendron tulipifera, Fagus grandifolia* and *Acer saccharum* have a greater abundance of reproduction, while on the north slope it is higher for *Acer rubrum* and *Tilia americana*.

The herb layers show a large degree of difference between the slopes. In terms of density, this difference is 72%. As with the other layers, the difference is due to the absence of certain species from the quadrats on one slope and to the large difference in the abundance between the slopes for other species. There is a large number of species (Tables 11, 12) which occur in the quadrats on only one slope. There are 19 herbaceous species which were present in the north slope quadrats but did not occur in the south slope quadrats. Ten of these were not observed growing in the south slope community. The other 9 species were found to be either uncommon, rare or very rare on the south slope. There are 42 herbaceous species encountered in the south slope quadrats which did not occur in the north slope quadrats. Over half of this number were not observed growing in the north slope community. The very large difference in total herb density between the slopes also adds to the degree of difference in this layer.

In the calculations, woody reproduction is included in the herb layer. Since this is true, the distribution and relative importance of shrub and tree reproduction under one foot in height affects further the difference between the herb layers on the slopes. From the data on this size class (Tables 8, 9, 10) it can be seen that there are 11 species which were found only in the north slope quadrats and 13 species found only in the south slope quadrats. General observations indicate these species to be rare in this size class on the opposite slope.

The bryophyte layer shows the greatest degree of

difference between the slopes. In terms of difference in cover, the value is 95% while for difference in frequency, it was 92% (Table 15). These values, together with an inspection of the data presented in Table 13, show the moss layer to be almost completely different on the two slopes. Part of this striking difference may be due to sampling error. However, study in the field over a period of a year and a half together with approximately 350 identified collections indicate that the bryophyte layers are indeed strikingly different. The difference is apparent in the bryophytes of all substrate groups, i.e. the soil, rock, deep crevice, wood, and bark inhabiting species. On the north slope, the bryophyte layer is better developed in all substrate groups, both in terms of numbers of species and cover.

DIFFERENCES IN THE LIFE FORM SPECTRA ON THE TWO SLOPES

Plant ecologists have long believed that the ability of a plant to survive is dependent upon its being adapted to the conditions of its environment. Several investigators have attempted to assign plants to various life form designations on the basis of certain "adaptive" features of plants. Of the many proposed life form classifications, that of Raunkiaer (1934) has received the widest use. In this system, only the spermatophyte species are considered. The species are assigned life form designations on the basis of the position of the perennating buds during the difficult season.

Such a classification has obvious weak points. Warming (1909) pointed out that a system based upon such criteria fails to take into account the response of plants to the growing season. In spite of such limitations, the simplicity of the classification has led to its wide use and we now have considerable data from various regions and habitats in the United States for comparison (Ennis 1928, McDonald 1937, Oosting 1942).

Four life form spectra constructed from the area studied are presented in Table 16 together with spectra published by other investigators. The spectrum for the flora of the entire ridge as well as that based upon only the species encountered in the quadrats shows the typical temperate region increase in hemicryptophytes over the "normal spectrum" of Raunkiaer (1934). The lower therophyte values in the present study do not conform, however, to regional temperate zone spectra such as that of Ennis (1928). This is due to the limitation in habitat type resulting from the exclusion of areas of disturbance such as recently cultivated fields.

Oosting's (1942) spectra for north and south facing bluffs in North Carolina show shifts in life form similar to those observed in the present study. However, in the shift in spectrum with slope exposure in North Carolina, Oosting reports higher ratios of spermatophytes to pteridophytes on the north facing bluff; in the present study the reverse was true. In discussing the differences in spectra between the two exposures, Oosting states that the spectrum for the south facing bluff suggests a therophytic or semi-

TABLE 16. Life form spectra of the total observed flora of the ridge, as represented by only those species encountered in the quadrats on the two slopes, and of the quadrat flora on each slope. Other published spectra are included for comparison.

Location	Number of Species	Ph	Ch	H	Cr	Th	Pterido-phyte Ratio
New Jersey							
Total observed flora of ridge...	229	31.0	1.3	48.5	13.1	6.1	13.5:1
Quadrat flora of ridge.........	138	34.0	2.1	44.9	12.9	5.8	19.7:1
North slope quadrat flora......	86	41.8	1.2	41.8	15.2	0	14:1
South slope quadrat flora......	112	32.1	1.8	46.4	12.5	7.1	37:1
North Carolina							
Oosting (1942) north slope.....	84	45.2	3.6	25.0	27.0	0	10.5:1
South slope.................	45	26.6	0	51.1	4.4	17.8	6.4:1
Connecticut							
Ennis (1928).................	1,453	15.0	1.9	49.4	21.7	11.7	.....
Indiana							
McDonald (1937).............	1,837	15.3	1.7	50.3	19.6	13.0	31.7:1
So. Quebec							
Dansereau (1943).............	346	17.0	10.0	56.0	15.0	2.0	....
Normal Spectrum							
Raunkiaer (1934).............	...	46	9	26	6	13	25:1

desert climate while that for the north facing bluff suggests a cryptophytic climate; he points out that Raunkiaer recognizes no such climatic region as the latter. Although the higher than "normal" therophyte values on the south facing slope in North Carolina may be interpreted as indicating a climate somewhat drier than the average for the region, the absence of therophytes from the north slope both in New Jersey and in North Carolina seems to be a wider departure from the normal spectrum than is the slightly higher percent on south facing slopes. The necessity for sunny open ground for the winter and early spring development of many therophytic seedlings may be important in precluding the widespread existence of these forms on north facing slopes. The spectrum for the Laurentian Maple Groves (Dansereau 1943) shows 2% therophytes for a region well north of the two areas in which the slope exposure studies were made.

PERIODIC CHANGES IN ENVIRONMENT AND VEGETATION ON THE TWO SLOPES

The data show that there is a marked seasonal variation in the magnitude of the differences between the slopes in both the vegetation and the environment. In an ecological study it is important that these two periodic complexes be considered together. Before such a synthesis is attempted, however, it is perhaps important to reemphasize the limitations on such studies. Thus, no thinking student of vegetation would contend that the rhythmic changes in environment have no effect upon vegetation. Likewise, none would hold that the cyclic changes in vegetation have no effect upon the environment. The two interact to such a point that it is practically impossible to separate cause from effect or coincidence

from relationship. Even in carefully controlled laboratory experiments it has not been possible to integrate all of the physical factors into a biologically significant physical factor complex. We certainly have no method of expressing the complex of compensations, cooperations, and competitions that characterize vegetation dynamics. Our methods of vegetation study often bring out differences in vegetation that owe their existence to chance alone or to some sequence of past events which current environmental studies could not hope to explain. Thus, the bringing together of these partial studies of periodicity in environment and these partial studies of periodicity in vegetation are not intended to show direct cause and effect. They are brought together in order that parts of these two variables may be viewed in the light of one another in the hope that in some instances it will be possible to approach an insight into the complexities that exist in the vegetation on a north and south slope in central New Jersey.

The observations on the differences in environment and in vegetation between the two slopes can best be studied together by presenting the data by seasons. These seasons are based not upon astronomical divisions but upon phenomena demonstrated by the vegetation itself. For the most part they are the same as those suggested by Wolfe et al. (1949).

WINTER

The winter season begins with the fall of the last leaves from the tree canopy. The change is not sharp, but can be said to occur within a week's time. Since the last major tree species to lose its leaves is *Quercus rubra*, an important tree on both slopes, winter comes by definition at the same time on both slopes. In 1948, this occurred in the second week of November and in 1949, in the third week.

At this change in seasons, there are marked differences in both the vegetation and the environment on the two slopes. As can be seen in Figs. 5 & 6,

the mean weekly soil temperature was around 5° F higher and the mean air temperature at 5 cm was 8 to 10° F higher on the south slope. Maximum air temperatures were considerably higher on the south slope while there was but little difference in the minima (Figs. 7, 8). The first freezing temperatures had already occurred on both slopes.

While the tree layers apparently become dormant on both slopes with this change, there are differences in the other layers of vegetation. On the south slope many grasses, sedges, and winter rosette plants are slowly producing new leaves and expanding those present. The widely scattered ferns and bryophytes are also green, but add little to the aspect of the vegetation. Many shrub species are slow in losing their last leaves, and hang on to some of them well into the middle of the winter. On the north slope, although the abundance of rosette plants, grasses and sedges is less, and although fewer of the shrubs are

FIG. 6. Mean air temperatures at 5 cm on the two slopes for the period from May 1948 to February 1950 at stations under light summer shade. Mean temperature is the average of the weekly maximum and minimum except for July and August where they are the weekly averages of the daily extremes.
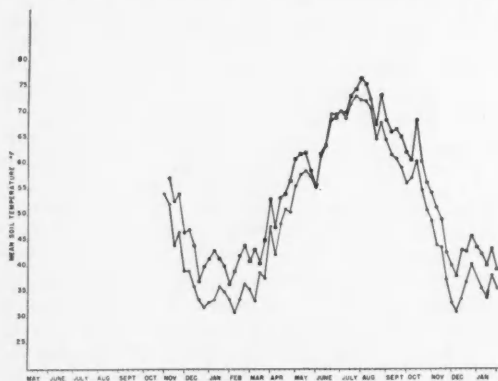
FIG. 5. Mean soil temperature at a depth of 4 cm on the two slopes for the period of November 1948 to February 1950 at stations under light summer shade. Mean temperature is the average of the weekly maximum and minimum. The upper curve connecting the squares is for the south slope.

FIG. 7. Maximum air temperature at 5 cm for the same period and stations as noted in Figure 6. The upper curve connecting the squares is for the south slope.
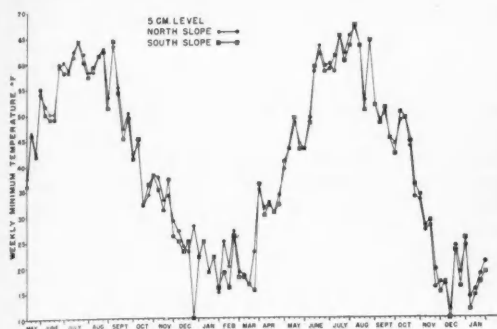
FIG. 8. Weekly minimum air temperatures at 5 cm on the two slopes. The data are for the same period and stations as noted in Figure 6.

FIG. 9. Ice storm damage to trees on the north slope. The storm occurred in December 1947.

tardy in losing their leaves, the ferns and bryophytes contribute considerably to the greener aspect typical of the north slope. The rocks not covered by mosses are a soft gray-green from a heavy cover of lichens.

Freezing temperatures do seem to play a major role in the death of foliage in some species. Individuals of *Adlumia fungosa* were observed to lose part of their foliage when the minimum air temperature dropped to 32° F. Other plants, such as *Aquilegia canadensis*, maintain young foliage until the ground freezes and the minimum air temperatures drop to 25° F. In many species in both communities, however, photoperiod is probably as important or more important than temperature in producing leaf fall. Matzke (1936) has shown this to be true for street trees in New York.

As the winter progresses, the soil and air temperatures decrease on the two slopes. In both years of observation, the mean weekly soil and air temtures on the north slope were below 40° F much of the winter (Fig. 5). Very little direct insolation is received below the 20-cm level at this season. The prevailing wind direction is northerly during the winter, and on many days the weather on the north slope is quite severe. On such days, the leaves of *Polypodium virginianum, Dryopteris marginalis* and many of the bryophytes are curled. The soil at 4 cm is frozen during a few weeks of the winter but at shallower depths, it is frozen for a much longer period. During the short warm periods in winter (Figs. 5, 6), the soil on the north slope may thaw and the bryophytes and ferns appear a bright green. Only one such winter "thaw," which occurred the last week in December 1949, produced any noticeable greenness in the rosette plants. At this time, the mean soil temperature exceeded 40° F for a few days.

Apparently some of the mosses are able to carry on growth under the conditions of winter on the north slope. In tufts of *Eurhynchium serrulatum*, capsules have swollen and calyptras have been pushed off during this season. It would be of interest to know whether cell division occurs during this increase in size.

Ice storms, which are frequent in this region, are almost always accompanied or followed by northerly winds. Since these winds strike the north slope with a fairly high velocity, ice storm damage to the tree crowns is much more severe on that slope. Other factors such as duration of ice on branches, etc., may also be important in causing more severe damage on the north slopes. Ice damage is thus in part responsible for the more open tree canopy on the north slope. Figure 9 shows the nature of some of the damage caused by these ice storms.

Snow covers the ground on the north slope for much longer periods than on the south slope. The longer lying snow cover on the north slope may raise the temperature minima at the lower levels above those on the south slope. In central New Jersey, however, the influence of snow cover in protecting plants from low temperatures is probably very slight due to the frequent lack of snow cover during cold waves.

On the south slope, the picture of winter is considerably different. Mean weekly soil temperatures at 4 cm are seldom below 40° F and reach up to 45° F, as in the last week of December 1949. Mean weekly air temperatures at 5 cm may exceed 40° F several times during the winter, and seldom are they below 35° F. Since the prevailing winter winds are northerly, air movement on the south slope is generally characterized by a gentle up-slope breeze. On all except overcast days, the high insolation angle warms the litter to where it actually feels warm. Only during the more severe cold waves does the soil remain frozen all day. Only on one occasion during the two years of observations was the soil frozen to a depth of 4 cm. Due to the almost daily thawing of the soil, many more freeze-thaw cycles are completed on the south slope.

Snow cover is not long lasting on the south slope. Even the rare deep snows that fall in this region last but a short time. In addition to the influence of the steeper angle of insolation on the south slope, the presence of large numbers of *Cornus florida* also seems to influence the rate of snow melt. During and after snow storms, many small flakes of periderm, primarily from this species, become incorpo-

rated with the snow. Apparently, due to the flakey nature of the periderm, pieces are carried down with the snow which falls from the branches. Other species undoubtedly contribute to the effect. When the snow begins to melt, the surface becomes dark with these particles. It seems probable that the change in albedo accelerates the melting. Even though the snow lasts much longer on the north slope, the effect is not so noticeable there, possibly due to the much smaller numbers of *Cornus florida*.

The vegetation of the south slope is much more active during the winter. Those plants with winter rosettes are more numerous on this slope. Many of these rosettes expand new leaves during the winter. The grasses and sedges show leaf elongation throughout the winter. These new leaves provide food for some of the fauna during this season, for there is ample evidence of cropped off leaves. Such foraging makes it difficult to obtain long records of growth in these species. Much of this growth probably is limited to the warmer days when the air temperatures may go up to 70° F at the 5 cm level (Fig. 7). In such warm spells, the less active rosettes such as *Hepatica americana* lose their red color and become bright green. As previously mentioned, some of the annuals germinate and produce several nodes during this season. Some of the widely scattered mosses produce or mature capsules during this season. *Atrichum macmillani*, *Thuidium virginianum* and *Eurhynchium serrulatum* mature spores during the early part of the winter. Several other species begin to elongate the seta during the middle and late winter.

In the fairly open winter of 1949-1950, the cold waves of late February and early March reduced much of this vegetative activity on the south slope. Several of the species that had produced considerable new foliage during the winter showed dead leaves following minimum temperatures of 6 to 10° F. No plants were observed to have been killed, but many of the larger individuals of *Cerastium nutans* in exposed places lost all except the lower two or three nodes. Later these individuals branched and continued growth.

Thus, the winter season produces sharp differences in both the environment and the vegetation periodicity on the two slopes. The more equitable environment on this slope during winter may well be a critical factor for some of the predominantly south slope species. The therophytes, in particular, would be a group well worth studying carefully from an autecological and ecological life history point of view in future studies of the dynamics of slope exposure segregation. On the other hand, the absence on the north slope of the relatively long mid-winter warm periods, that could induce premature vegetative activity, may be a factor favoring the segregation of some of the predominantly north slope species. Experiments with certain of the geophytes might be of interest in this connection.

SPRING

The change in seasons from winter to spring has been defined as the period when vegetative activity shows a marked increase near the surface and under the litter (Wolfe *et al.* 1949). Such an increase in activity was observed to begin on the south slope by the first week in March in 1949, but not until after the second week in 1950. On the north slope, it occurred nearly three weeks later. In 1949 this change in seasons on the south slope followed a period of warm weather in late February (Figs. 5, 6) when the mean weekly soil temperatures reached 44° F. In the first week of March when the activity was observed, the mean soil and air temperatures were 41°F and 40.5° F, respectively. On the north slope at this time there was 15 cm of snow cover. Some snow cover was present over this slope until the middle of the third week in March. With the disappearance of the snow, vegetative activity began on the north slope both in the litter and in the lower growing shrubs. On the north slope then, there seems to be little difference in the time of occurrence of the events chosen by Wolfe *et al.* (1949) for distinguishing between early and late spring (the initiation of vegetative activity under the litter as opposed to initiation of vegetative activity in the buds of woody plants above the surface). It is of interest to note that Hopkins & Murray (1932) have chosen only phenomena occurring in woody species for marking the change of seasons. This would tend to reduce considerably the influence of microclimatically induced variation in regional phenological studies.

With the disappearance of the snow cover on the north slope, and the increasing soil and air temperatures, vegetative activity begins to accelerate. On the surface, the bryophytes show considerable activity. Most of the herbs grow slowly at first. A few species flower, such as *Hepatica americana* and *Anemonella thalictroides*, the former nearly two weeks behind those on the south slope. The shrubs begin to leaf out, or flower, only slightly behind those on the south slope. At this time, the weekly mean air temperatures at 1 m as well as the soil temperature at 4 cm have reached 40° F, and remain above this level until November (Figs. 5, 6).

The six weeks following the sharp increase in vegetative activity in the shrub layers mark a period of rapidly increasing temperatures and plant growth on both slopes. The differences between the slopes in soil and air temperatures show a slight increase during this period, particularly toward the latter part. Minimum air temperatures of 32° F occurred near the surface during most weeks until the first week in May (Fig. 8). No frost damage was observed, however, in any of the many vigorously growing species.

In spite of the earlier start obtained by the herbaceous vegetation on the south slope, this layer seems to reach its peak of development earlier on the north slope. Toward the end of the spring season many of the important species on the north slope are either about to bloom, in bloom, or in fruit. On the south slope, a greater proportion of the herb layer is made up of species that have their grand period of growth during the early summer.

In the tree layer two aspects of spring vegetative activity, leaf expansion and cambial activity were observed. The stems of the oaks were increasing in radius by April 1, but leaf expansion did not start until after April 15. The stems of Liriodendron, on the other hand, did not start to increase steadily in radius until the first week in May. A very slight increase was noted in the third week in April but none in the last week. Leaves of this species were expanded one inch on April 15. Lodewick (1928), in central New York state, observed that the initiation of cambium activity in *Quercus velutina* was separated from leaf expansion by about two weeks while in Liriodendron the two phenomena began about the same time. In general, the rate of radial increase in the oaks observed on the south slope was greater during the spring months than in the oaks observed on the north slope (Fig. 4). This difference may be related to the higher soil and air temperatures observed on the south slope at this time (Fig. 5, Table 2).

Thus, the spring season is characterized by the existence of rather sharp differences between the environments and the vegetative activity on the two slopes. The early initiation of favorable growth conditions near the ground on the south slope, with the resultant increase in precanopy-closure growing season, may be important to the life cycles of some of the predominantly south slope species. Conversely, the absence on the north slope of higher soil and microclimatic air temperatures with the occasional mild and brief drought conditions may explain the virtual restriction of some of the early spring plants such as *Anemonella thalictroides* to that slope of the ridge. The autecology of some of these species completing most of their seasonal cycle in the spring is fertile ground for future slope exposure studies.

SUMMER

Spring ends and summer begins with the "closing" of the vegetative canopy (first and second week of May in years studied). This does not signify that all tree species have fully expanded their leaves, for *Quercus velutina* and *Q. rubra* are not fully expanded for another several days. This criterion for the beginning of summer (Wolfe *et al.* 1949) differs from that of Hopkins and Murray (1932) who use the completion of leaf development of Quercus to mark the beginning of summer. In both years of observation, the weekly mean air temperature at 5 cm was about 62° F on the north slope and between 73° F and 77° F on the south slope when the canopy closed. Weekly mean soil temperature, available only for 1949, was 55° F on the north and 61° F on the south slope for this time (Figs. 5, 6).

In the first week or so of summer, the last tree species had completed leaf expansion. In the oaks, a sharp drop occurred in rate of radial increase, between the closing of the canopy and June 4. This decrease is probably a complex reaction due in part to the natural cycle of the tree, and aggravated by a period of cool weather (Figs. 5, 6). The weekly mean soil temperatures dropped from 58° F and 62°

F on the two slopes during the third week of May to 55° F and 56° F in the first week of June. During this period, the minimum temperatures did not drop below 39° F under the canopy. At the U. S. Weather Bureau station ten miles south southwest of the area, however, minimum temperatures dropped below 32° F. It is probable that such low temperatures also occurred in the top of the tree layer at this time.

The herbaceous layers on both slopes make considerable growth in the first few weeks of summer. Following this, the herbaceous layer on the north slope seems to attain a sort of dynamic equilibrium. A few of the early species begin to decline; a few of the later species are still growing rapidly; many of the species have passed their grand period of growth and are growing more slowly. On the south slope, however, the herbaceous layer in general continues to grow rapidly.

The summer season brings out sharp differences in water relations on the two slopes. Although the difference in angle of insolation between the slopes is less during the summer than at other seasons, this difference is great enough to produce critical differences in the environments of the two slopes. Air and soil temperatures are higher and the atmosphere is drier on the south slope (Table 5, Figs. 5, 6). Adding to these differences, the prevailing summer air flow is southerly, resulting in greater air movement on this slope. These factors combine to produce a much higher water requirement. Even in regions of high summer precipitation, evaporation and transpiration utilize soil moisture so rapidly that drought conditions exist much more frequently on south slopes. In central Indiana, Potzger (1939) found that during a summer in which an average of one inch of rain fell per week, the soil moisture at 6 in. dropped below the wilting coefficient on the south slope four times. On the north slope, it dropped to this level but once. In 16 of the 20 weeks in which Potzger sampled these slopes, the soil moisture content was 30% or more (in reference to dry weight of soil) on the north slope. On the south slope, the soil moisture reached this value but four times. In more arid regions such as Colorado (Bates 1923) and Idaho (Gail 1921), the difference in frequency, length and severity of drought is also great between the slopes.

In the present investigation, although no study was made of soil moisture, daily observations made while digging up the soil thermometers indicate the south slope to have dry soil at 4 cm more frequently and for longer periods.

On south slopes, soil moisture may be near depletion at a time when water requirement of vegetation is high. The Livingston atmometer has been used by several investigators for measuring the difference in evaporating power of the air on slopes of different exposure (Gail 1921, Potzger 1939, Aikman 1941). Potzger has shown that on a forested ridge in Indiana, the evaporation from atmometers was 60% greater on south than on north slopes. The height

of these observations, not specified, was probably within 1 m of the forest floor.

The differences between the slopes in soil and air temperatures observed in the present study indicate that temperature is an important factor in producing the difference in water requirement between the slopes. The average maximum air temperature could be up to 4° F higher at 2 m on the south slope, while at 5 cm, the difference might be over 7° F. During the latter part of the summer, the maximum soil temperatures at 4 cm may be 7° F higher on the south slope. These differences in temperature should result in both increased evaporation and transpiration on the south slope so long as water is available.

The study of atmospheric moisture made during the summer of 1948, is in agreement with other studies indicating the south slope to have drier air (Gail 1921, Hayes 1941). While the vapor pressure was approximately the same on the two slopes, the midday vapor pressure deficit was somewhat higher at all levels on the south slope. The difference in vapor pressure deficit between the slopes may well influence transpiration. It would seem of importance to point out, however, that until the air is saturated, transpiration by the vegetation also influences the vapor pressure deficit of the air within these layers of vegetation.

The difference in wind between the slopes has been mentioned. Air movement is much greater on the south slope. Potzger (1939) indicates the same to be true on south slopes in Indiana. Wind, through its influence upon mixing and carrying off water vapor, may markedly influence both evaporation and transpiration.

These differences between the slopes in temperature, atmospheric moisture and wind were observed under the forest canopy. The plants which exist in these layers on the two slopes were observed to show marked differences in response to the rather severe summer drought of 1949. On the north slope, *Prunus virginiana* lost almost all its leaves in late August, *Aquilegia canadensis, Polypodium virginianum, Arisaema triphyllum, Asarum canadense, Cimicifuga racemosa, Clematis verticillaris* and *Rubus odoratus*, all species important on the north slope, were found to be wilted during the hottest part of the drought days. Other species such as *Adiantum pedatum* had many individuals that lost their above-ground parts as a result of the drought.

On the south slope, the occasional individuals of the species mentioned above were found to suffer much more from the drought. Many plants died, others recovered with the coming of rain. *Cimicifuga racemosa* which was in flower during the drought failed to set seed over much of the south slope. For the most part, species characteric of the south slope seemed to suffer less.

The differences between the slopes in air temperature and atmospheric moisture have been shown to be greatest near the surface. Hayes (1941), Byram (1948) and others have shown that the moisture content of the litter and duff is higher on north facing

slopes. Byram pointed out that on steep north slopes, due to radiation cooling, the litter is colder than the air during the day as well as at night. On occasions the air may actually give up moisture to these colder surfaces even during the day. How important such a source of moisture might be to the terrestrial bryophyte layer on the north slope is not known. However, whether any large quantity of water is thus obtained during the summer or not, the improved water balance due to lower temperatures, lower light intensity, and higher atmospheric moisture is probably of considerable importance in permitting the much greater development of this layer on the north slope. It would seem probable that the rock-inhabiting species would be influenced the most. The much higher frequency of sporophyte production on the north slope in some species may also be related to these differences. These differences near the surface on the two slopes could be as important for any layer of vegetation since all seedlings must pass a critical period under its influence.

In addition to the differences in physical environment observed under the canopies on the two slopes, above canopy differences must also be assumed to exist. Geiger (1950) has described how a layer of vegetation deactivates the normal active surface, the top of the vegetation layer then becoming the region of sharp gradients of temperature, humidity and wind. As pointed out previously, deactivation is not complete on the south slope while on the north slope it is more nearly so. Nevertheless, large areas of the upper surface of both canopies must be characterized by gradients similar to those observed by Geiger. Since the angle of insolation striking those upper surfaces is not the same on the two slopes, differences in intensity of these gradients probably exist.

On the south slope, due to the penetration of considerable insolation to various depths of the vegetation layer, the active surface has a varied topography. This would seem to favor the exaggeration of gradients as described by Geiger for small clearings; such an effect would be less on north slopes. Although no observations were made in these upper layers, it would seem probable that slope differences in surface temperatures of the vegetation, air temperatures and atmospheric moisture would exist. The difference between the slopes in air movement would also be considerable at this upper layer due to the prevailing southerly winds during the summer. These probable differences in the upper canopies of the two slopes as well as those observed below the canopies would affect the tree species. Measurements of change in radial dimensions made during the growing season of 1949 indicate a difference in response to drought conditions between the two slopes. The trees on the south slope were more sharply affected by the rainless periods.

High maximum temperatures at the soil surface have been held to be one of the important factors in the segregation of plants on north and south exposures. Bates (1923), working in Colorado, reported

heat lesions on the tender stems of certain tree seedlings where the hot soil surface of south slopes was in contact with them. Platt (1951), working on the shale barrens in the mid-Appalachians, reports seedling injury on steep south facing shale slopes. At the time of injury he recorded surface temperatures of 60° C. In the present study, no evidence of this sort of damage was found. Due to lack of adequate instrumentation, no study was made of surface temperatures. It seems probable, however, that in the communities studied they would seldom reach the level necessary for such damage to tissue.

Undoubtedly, the summer season produces other differences that were not observed in the present study. Preliminary observations made during the summer of 1952 in northeastern Virginia indicate that the soil and litter flora and fauna may be quite different on north and south slopes. These differences were associated with exposure-induced differences in soil and litter moisture and temperature as well as in substrate acidity and mineral composition. The latter two apparently result from dissimilar vegetation and organic layers on the two slopes since hemlock is abundant on the northern exposure and oak-hickory characterizes the southern exposure. It should also be pointed out that these different soil and litter populations may, in turn, exert some selective action upon certain of the higher plant species that tend to segregate on north and south slopes.

The summer season, then, produces smaller differences between the slopes in microclimatic air temperature and soil temperature than at other seasons of the year. However, the differences observed below the canopy plus the differences that must be assumed to exist at the upper surface of the tree layer operate to produce the greater moisture stress on the south slopes, as opposed to north slopes, that has been reported by several investigators. This difference in the severity of summer drought is undoubtedly a very important factor in the segregation of species on the two slopes. Experiments on the relative drought resistance at all stages of the life and seasonal cycles of the more exclusive species offers a promising line of investigation for future exposure studies.

FALL

The change in seasons from summer to fall is marked by the onset of true autumn coloration in the foliage. The time of this change is difficult to fix due to the difference in time of onset of coloration between the various species, and even between individuals of the same species. The effects of late summer drought further complicate the problem of fixing a time of appearance of true color. In 1948, onset of coloration occurred during the third week in September, while in 1949, probably due to the late summer drought, color appeared in the second week. The mean air temperature at 5 cm had dropped to 60° F on the north slope and 70° F on the south slope, while the absolute minimum air temperatures below the canopy were in the mid-forties on the two slopes. Mean soil temperatures at 4 cm were approximately the same as the mean air temperatures at this time.

Although coloration appears at the same time on the two slopes, it develops more rapidly on the north slope. Leaf fall shows the same relationship to the two slopes. This difference is not due to any direct influence of the environment upon coloration and leaf fall, since there is little constant difference between individuals of the same species on the two slopes. Rather, it is due to the difference in abundance of the various species between the slopes. On the north slope, both the herb and tree layers contain a greater abundance of species which develop color and lose their leaves more rapidly. On the south slope, the herb layer has many flowering species at this season, while on the north slope only a few species are in bloom.

As the fall season progresses, the tree, shrub and herb foliage thin out and the terrestrial bryophyte layer on the north slope appears much more prominent. Several species of mosses mature their spores at this season. On the south slope, this layer is almost insignificant; a few species, however, produce spores in the fall.

During this season, the minimum air temperatures are slightly lower on the north slope than on the south. This is probably due to the more rapid thinning of the tree canopy on the former slope. No difference was noted between the slopes in the time of occurrence of the first frost. In 1948, the temperature dropped to 32° F in the third week of October, while in 1949 this occurred in the fourth week. The mean air temperature at 5 cm at this time was about 50° F for the north slope and 60° F for the south slope. Mean soil temperatures were 51° F and 56° F respectively.

Although the latter part of the fall season produces the greatest differences in air temperature between the slopes of the year, the differences in vegetation periodicity seem to be the least at this time. Though smaller than at other seasons, the differences in the terrestrial bryophyte layers are greater than in the other layers. On the north slope this layer is green and prominent; on the south slope it is very spotty and often dried up. Since no study was made of below-ground plant parts or of the forest fungi, the lack of difference in vegetation periodicity may be more apparent than real.

The difference in forest fire danger between the north and south slopes has been described by Hayes (1941), Byram (1948) and others. Fire danger is much more frequent and lasts much longer on south slopes. This difference between the slopes is often ignored by students of vegetation. Even though fire may have occurred nearly as frequently on two closely adjoining slopes such as those in the present study, the higher moisture content of the fuels on north slopes undoubtedly results in lower fire temperatures. Actual fire damage to the vegetation is probably less on north slopes, particularly to the plant parts in the surface of the soil.

The latter part of the fall season produces many fires in the northeastern deciduous forest. It is at

this time that the differences in air and soil temperature and probably forest fuel moisture are greatest. Also, the prevailing wind at this time is southerly. It is entirely possible that these large environmental differences have, through their influence upon fire damage, operated to produce some of the differences observed in the present vegetation on the two slopes.

Thus, the difference in the amount of insolation striking the surface of the north and south facing slopes produces differences in temperature and moisture structure in the microclimatic layers and in other factors of the physical environment. These differences are further modified by the influence of the vegetation on the two slopes. Just what portion of the differences observed in the physical environments is caused by the vegetation cannot be determined from the present investigation. Regardless of whether the differences are primarily a result of the exposure or a secondary effect of the vegetation, they can be said to influence in part, to a greater or less degree, the composition, structure, periodicity and vitality of the plant communities. These influences upon the plant communities work through the responses of the individual plants as they exist, not as separate entities, but as components of the complex of compensation, cooperation, and competition of the entire biotic community. The individual factors contributing to the segregation of species on north and south slopes are many and overlapping. Some factors such as lethal surface temperatures, snow cover, etc. influence plants at one season only; others such as substrate moisture may operate throughout much of the year. Some factors such as fire or ice storm damage may operate only on rare or occasional years, others operate every year. It seems clear that future studies of the problem of exposure-induced segregation of plants should include coordinated observations of both the environment and the various periodic phenomena such as germination, initiation of growth, flowering, fruiting, dormancy, etc. of the more exclusive species. Obviously, all seasons of the year should be considered. Such studies, supplemented by laboratory investigations of the tolerance ranges of these plants to the various factors, for each phase of their life and seasonal cycles, would be valuable contributions to our knowledge of plant ecology.

SUMMARY

A study was made of the vegetation and the microclimates on the north and south facing slopes of a ridge in central New Jersey. The ridge is of diabase rock and has a maximum elevation above the surrounding country of approximately 600 ft. The field observations were made during the years 1948 to 1950.

The difference in the amount of incoming insolation on the two slopes produces markedly different microclimates. In general, the south slope is characterized by two types of daytime microclimatic air temperature structure. Under heavy shade, the air temperature profile is almost isothermal in the lower 2 m.

Under light shade, in small openings in the tree canopy and, in general, during the leafless season, the air temperature profile in the lower 2 m is characterized by sharp changes with height, the highest daytime temperatures being found near the ground. On the other hand, the north slope microclimatic layer is characterized by a decrease in air temperature toward the ground at all seasons. Even fairly large openings in the tree canopy do not materially influence this relationship.

Atmospheric moisture studies made during the growing season indicate that while the vapor pressure deficit decreases toward the ground on both slopes, it does so more sharply on the north slope.

These differences in the structure of the microclimatic layers on the two slopes are such that when the microclimates of the slopes are compared by layers, the differences between the slopes increases in magnitude toward the ground, i.e. the greatest differences in microclimate between the slopes were found at 5 cm, the lowest level observed, while the smallest differences were found at 2 m, the highest level observed.

The structure and composition of the vegetation on the two slopes were also found to be quite different. Few species were found to be absolutely exclusive to either slope, rather, the differences were found to be due to the shifting in the relative density, frequency, and cover of the species. As with the microclimates, the magnitude of the differences between the slopes tended to increase toward the ground. The greatest differences in vegetation were found in the terrestrial bryophyte layers, the smallest differences were found in the main tree layers.

The magnitude of the differences between the slopes in soil temperature, microclimatic air temperature and in the periodicity of the vegetation were found to vary with the seasons of the year. However, the greatest differences between the slopes in these environmental factors did not occur at the same season as did the greatest differences in periodicity of the vegetation. Environmental differences reached a maximum in the fall while periodicity differences were greatest in spring. The smallest differences between the slopes in the environmental factors observed were found in the summer.

The investigation indicates that further progress on the problem of segregation of species on slopes of different exposure may be made through studies of the ecological life histories of some of the more exclusive species. Emphasis should be placed upon their relationships during the fall, winter and spring seasons. On south slopes the therophytes are of particular interest while on north slopes, the geophytes seem to offer the best choices.

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COMPOSITION OF UPLAND SECOND GROWTH HARDWOOD STANDS IN THE TENSION ZONE OF MICHIGAN AS AFFECTED BY SOILS AND MAN[1]

JACK C. ELLIOTT

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INTRODUCTION

There are two expressions of the deciduous forest formation of eastern Northern America reported for the state of Michigan. One is the Beech-Maple forest in the southern part of the lower peninsula. The other is the Hemlock-White Pine-Northern Hardwood forest in the upper part of the lower peninsula and throughout the upper peninsula (Fig. 1).

The boundary between these two regions is not sharply defined. Braun (1950, p. 338), Potzger (1948, 1946), Darlington (1945), Veatch (1931), Gleason (1924), Quick (1923), Livingston (1903, 1905), Whitford (1901) and Beal & Wheeler (1892), as well as others, have pointed out the presence of this tension zone. Here, relics of the northeastern conifer forest mix with northern elements of the deciduous forest. This transition is usually described as being located near latitude 43° N.

The portion of the Hemlock-White Pine-Northern Hardwoods region north of this tension zone has been considered to form a part of the mixed conifer-northern hardwood forests of northeastern North America, and it has been discussed by ecologists and plant geographers more voluminously than has any other forest formation on the North American continent. A number of descriptive terms have emerged from their studies which have been used to typify this region. The region to be discussed in this paper lies within the Northern Hardwood Forest of Frothingham (1915); as well as in the Northeastern Tran-

sition Forest region of Nichols (1935) and the Great Lakes or South Canadian Forests of Hardy (1920). It is likewise within the St. Lawrence-Great Lakes region of Harshberger (1911) and is included in the Lake Forest region of Weaver & Clements (1938, p. 496). In Braun's Deciduous Forests of Eastern North America (1950, p. 337), the area is called The Great Lake Section of The Hemlock-White Pine-Northern Hardwoods Region. Nichols (1935), Cain (1935) and Braun (1950) have reviewed the extensive literature of this region.

While a transition zone between two large vegetation cover types has always presented a tantalizing aspect of vegetational characteristics, little ecological work has been done during the last quarter century on the nature of the composition of second growth forest communities which are now representative of the deciduous forests in the vicinity of this tension zone. Opportunities for studies in undisturbed stands within the Hemlock-White Pine-Northern Hardwoods region in the northern part of the northern peninsula of Michigan are now nearly non-existent. However, to establish the nature of the present composition of the forest community in the northern portion of the transition zone, a quantitative study was made of upland second growth hardwood stands in Missaukee County (Fig. 1).

Primary objectives of the study were: first, to study quantitatively the composition of the upland second growth hardwood stands; second, to compare soil relationships with present vegetational composition of the stands; and third, to compare present
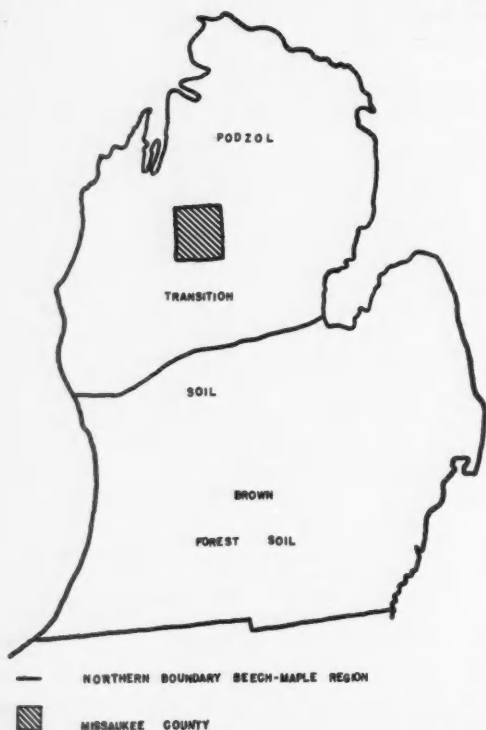
FIG. 1. Map of the lower peninsula of Michigan showing the location of Missaukee County; the northern boundary of the Beech-Maple Region (after Braun 1950); and major soil groups (after Veatch 1931).

composition of the upland second growth stands with vegetational patterns as revealed from an interpretation of field notes and maps of the original land survey.

The writer is indebted to Dr. William B. Drew for his advice and suggestions during the field work and preparation of the thesis.

DESCRIPTION OF THE AREA

LOCATION

Missaukee County is located in the north-central part of the lower peninsula near the geographical center of Michigan (Fig. 1).

PHYSIOGRAPHY

Moraines, till plains, and outwash aprons characterize the topography of Missaukee County, with the former the most prominent.

The southwest corner of the county is covered by a ridged deposit, of the knob-basin type of topography, which marks the northern terminus of the Lake Michigan-Saginaw Interlobate tract (Leverett 1924). A part of the Lake Border moraine extends northeastward across the central and northeastern part of the county. Near the center of the county is a ridge, a southeast extension of the main moraine. This

ridge, known as the Lake City-Harrison ridge, ends at the West Branch moraine near Harrison in Clare County. Relief of the moraine varies from 50 to more than 500 ft. Within the border of the moraine, however, average relief is about 100 ft. The topography of the broad summits of the ridges varies from slightly undulating and rolling to rough and knobby.

East and north of the northern terminus of the Lake Michigan-Saginaw Interlobate tract, as well as east and north of the Lake City-Harrison ridge, are extensive till plains. In the northeastern part of the county, and near the base of the morainic systems, are extensive outwash aprons. The topography of the till plains is undulating to rolling and on these are the better agricultural areas of the county. Outwash aprons are flat to undulating and their soils are rather poor.

CLIMATE

Missaukee County is located within an area in which climatic factors have favored development of forests (Whitford 1901; Seeley 1917; Quick 1923; Gates 1926; Darlington 1945; Potzger 1946, 1948; Braun 1950).

An examination of available climatological data for Michigan (U. S. Department of Commerce) indicates that Missaukee County compares favorably with the general area as regards temperature and length of the growing season. The county has slightly less rain annually. This difference, however, is not believed to be large enough to be a critical factor as regards distribution of the forest community within this area.

The physiography of the county is of such a nature that the "microclimate of edaphic factors" (Potzger 1948) would undoubtedly affect the vegetational expression, sometimes favoring species characteristic of the Beech-Maple region and at other times favoring species characteristic of the mixed conifer-northern hardwood region. Small fluctuations in temperature and moisture, factors which would be influenced by such microclimate-edaphic differences, would find expression here although they would not be evident within the boundries of the major communities. Determinations of such microclimatic-edaphic factors and their effect upon the vegetational distribution within the area are yet to be worked out. All that can be done at this time is to take notice of their probable existence and attempt to correlate plausible explanations when an analysis of vegetation seems to indicate that such factors are operative.

SOILS

The soils of northern Michigan are a part of the great soil group known as podzols (Fig. 1). These soils, developed from glacial drift, usually show considerable heterogeneity over a comparatively small area. Missaukee County soils are no exception. The legend of an unpublished Land Type Map for the county* lists no less than 22 major soil types and

* Land Type Map, Missaukee County. Agricultural Experiment Station, Michigan State College. Conservation Institute and Soil Science Section, Department of Conservation, State of Michigan; USDA, Bureau of Plant Industry, Division of Soil Survey. 1942.

associated with each major type are numerous minor types. Thus the final picture for the county's soils becomes a complex. Following location of 98 stands of upland second growth hardwoods for quantitative sampling, a check was made with the map to determine soils representative of the area. This check indicated the presence of six soil series: Arenac, Emmet, Kalkaska, Nester, Selkirk and Roselawn. Field notes covering the general description and profile development of the soils within the stands, when compared with the descriptions of the Established Soil Series[†], supported classifications of the land map.

According to The Division of Soil Survey (1939), the Arenac soil series consists of podzols developed in sands deposited by winds and water over heavy clay. The A_{00} horizon is most variable in the area of the nineteen quadrats on Arenac sandy loam. It is absent in some places where there is only bare sand at the surface; elsewhere it is composed of leaf litter an inch in thickness. Where the leaf litter is absent there is no humus layer; where the leaf litter is present there is a weakly developed brown raw humus. The A_2 layer is well developed with strong podzol characteristics. This layer is a loamy sand, light-lavender in color and varies from 3 to 9 inches in thickness. Loamy sand, slightly acid in reaction and pale coffee brown, is present in the upper part of the B horizon. Its thickness varies from 8 to 12 in., with the deepest layers in sites having the thickest A_{00}. A B_2 layer is more sandy than loamy and averages six inches in thickness. It has the same acid reaction as the B_1. The deepest layer of the B horizon is extensively developed, ranging from 1 to $1\frac{1}{2}$ ft. thick. It is yellow sand, neutral in reaction. There are some sample plots which contain, in addition to the yellow sand, a slightly mottled rusty-brown sand. The parent material is calcareous clay, which probably was water laid, as these tracts are physiographically outwash aprons.

Most of the sample plots are on the Emmet complex. This soil includes podzols developed from sandy, mostly coarse, glacial till. The solum varies from medium to strongly acid with parent material slightly calcareous, according to The Division of Soil Survey (1943). Profile character varies within the plots, especially in the A_{00} layer. In some stands it is nearly four inches thick, while at other places it is exceedingly thin. There is a typical mull humus layer, about 2 in. thick, in nearly every plot. The zone of eluviation is a loose, loamy sand, mostly pale-lavender in color, and usually eight inches deep. Three layers are distinguishable in the B horizon. The B_1 is sandy loam mostly light brown. However, in some instances this layer is somewhat yellowish. While variable in thickness, within the plots, its average depth is 10 in. A B_2 layer has the greatest variation in color characteristics within the sampling area. In some instances it is a mottled brownish-gray, in

† Division of Soil Survey, Bureau of Plant Industry, Soils and Agricultural Engineering, Agricultural Research Administration, United States Department of Agriculture. Copies on file with The Soils Department, Michigan State College, East Lansing.

others the color is reddish-brown. The loamy sand is without structure, slightly acid, and 4 to 5 in. thick. A B_3 layer, which is almost 2 ft. thick, has a greater clay content and with the sand, produces a coarse, somewhat blocky structure. This layer is low to medium acid in reaction. A moderately compact, slightly calcareous glacial till forms the C horizon. The Division of Soil Survey (1943) indicates that the $CaCo_3$ content of this horizon varies from 5-15%.

Kalkaska sandy podzols make up the third soil series. The Division of Soil Survey (1950) describes the series as being composed of sandy podzols developed on glacial outwash plains. They are sands of mixed composition possessing both silicate and limey materials. In the samples collected during this study, there is an A_{00} layer which varies from less than $\frac{1}{2}$ to 4 in. in thickness. The A_0 layer is composed largely of organic debris in various stages of decomposition tending toward humus, but less than humus. Its average depth is 1 in. The deepest layer of the A horizon is made up of a pinkish-gray, fine sand which averages nearly 1 ft. in depth. Digging "soil wells" through this layer was hampered by the accumulation of many secondary roots from the tree and shrub species. A fine loamy sand, dark brown in color and medium acid in reaction forms the B_1 layer of the B horizon. This layer is approximately 10 in. thick and has a granular structure in many of the plots. A B_2 portion is dry, brown, loamy sand, varying to a yellowish-brown sand, which is moister. This layer is like the B_1 in structure, thickness and reaction. Parent material is a light-brown to yellowish sand and varies from slightly moist to dry with many small stones.

According to The Division of Soil Survey (1946), the Nester series consists of podzols developed in moderately heavy, pinkish-brown glacial till, which is somewhat calcareous, with a solum acid in reaction. The A_{00} layer of the profile averaged 2 in. in thickness. The A_0 horizon is about 1 in. thick. In the A_1 layer of the horizon characteristics of a mull humus are easily identifiable. This layer, in these stands, is nearly 2 in. thick. Below, in the zone of eluviation, there is a light-gray loam about 4 in. thick. Upper layers of the B horizon consist of a yellowish-brown loam, some 3 in. thick. A B_1 layer is a fairly compact gritty clay loam, reddish in color and 2 ft. deep. The B_2 layer, while not sharply defined, is thicker than the preceding layer. The C horizon is composed of gritty, peddly clay till, limey in character, which has a reddish-pink cast.

The Selkirk series is composed of imperfectly drained soils which have been developed over reddish or pinkish calcareous till or lacustrine clay, in the podzol region, according to the Established Soil Series prepared by The Division of Soil Survey (1946). Stands of second growth upland hardwoods occurring within this series were on Selkirk silt loam. A consolidated soil profile consists of an A_{00} layer averaging about 3 in. in thickness. The A_1 layer has a typical mull humus. It is slightly thicker than the A_{00} layer. A podzol characteristic is evident in

the A_2 layer, which is silt loam, light-grey in color, and medium acid in reaction. Two layers are distinguishable in the B horizon, both giving visible evidence of imperfect drainage. The B_1 is a silty clay loam, reddish to yellowish-brown, and very coarse-structured. Its thickness varies from 7 to 2 in. In the B_2 layer there is a gray silt along with a reddish clay which is quite impervious and acid in reaction. The parent material forming the C horizon is a silty clay which, in some locations, is very pebbly.

Roselawn, is characterized by The Division of Soil Survey (1946) as including podzols developed on light-textured glacial drift composed largely of quartzone material. An A_{00} layer of Roselawn sand, which represents this series within the area studied, is variable in thickness. In its greatest depth, it is rarely more than 1 in., and in many stands the forest floor has a sparse covering. The A_0 layer is $1\frac{1}{2}$ to 2 in. thick, in some instances grading into at A_1 layer only slightly more decomposed. In other stands, where the A_{00} is heaviest, and the A_0 much decomposed, the A_1 layer contains a humus layer characteristic of the mor type. The illuvial portion of the A horizon is incoherent sand of a light-gray color, which varies from 4 to 10 in. in depth. A light-yellow loamy sand, 8 in. thick, forms the B_1 layer. The B_2 layer, less sharply defined, tends to lose the loamy yellow characteristic and to become quite loose sand. The parent material, about $1\frac{1}{2}$ ft. from the surface, is mostly sand. In some sample plots, gravel occurs in the C horizon, while in two "soil wells" there are reddish clay deposits in the gravel.

METHODS

General

Selection of stands of upland second growth hardwoods was made on the basis of the following criteria: 1) that they be representative of the upland land type (i. e., comprised of broad long slopes, sharp ridges, knobs and basins, swells and swags, and in places a succession of short slopes and swells producing a choppy and billowy topography); 2) that they represent natural stands (not planted); 3) that they must be as little disturbed as possible (fire, grazing and extensive cutting). Location of stands without disturbances from grazing and extensive cutting was most difficult. Stands (woodlots) which show no browse line and which are not used to supplement the winter fuel supplies are an exception to the rule. Because of these two factors, it was decided to treat quantitatively only the tree and shrub layers composing the vegetation of the selected sites.

Actual selection of stands was made during a reconnaissance through the county. Stands meeting the criteria were sampled quantitatively. In this manner 98 stands, rather evenly distributed through the western three-fourths of the county, were chosen and data from 546 5 x 20 m quadrats recorded.

Field Methods

Rectangular quadrats, 5 x 20 m, were laid out in each plot. However, because of different sizes of the woodlots varying numbers of quadrats were used in each to insure adequate sampling. In smaller woodlots, four quadrats were used; in the larger, 6 to 8 were employed. When the shape of the woodlot permitted, the quadrats were placed in line, with 20 m separating them. At other times two rows were established, with a 20 m interval between rows as well as quadrats. They were always placed far enough within the canopy to avoid bordering effects.

All trees and shrubs, 1 ft. or taller, were recorded on standardized data sheets which listed the species on the basis of the following size classes: Size Class Two, .09 in. d.b.h. or less; Size Class Three, 1.0 - 3.5 in.; Size Class Four, 3.6 - 9.5 in.; Size Class Five, 9.5 - 15.5 in.; Size Class Six, 15.6 in. and above. Nomenclature is that of Gray's Manual of Botany, 8th Edition (Fernald 1950). Records were kept of conditions of the forest floor, of any unusual physical appearance in the stands, and of any pertinent remarks contributed by the land owner. Soils were sampled by means of "soil wells" dug into the C horizon. One face of the well was scraped clean and measurements and descriptions recorded. Soil reactions were measured using a "Soil-Tex" kit. A soil well was dug in each stand, except on moraines. Here, the wells were placed on the crest, the slope and near the base.

Treatment of Data
Structural Character

Quantitative Descriptions: The present composition of the upland second growth hardwood stands, based on the quadrat studies, is described quantitatively in terms of frequency, density, basal area, and Density-Frequency-Dominance Index (Curtis 1947) as defined below.

Frequency is used here in the usual sense as the percentage of the total number of quadrats sampled in which the species is found.

Density, as used in this study, is a quantitative measure of the species abundance expressed on a percentage basis. It is determined by dividing the actual number of individuals of a species by the total number of individuals of all species within the sampling area.

Basal area designates important species from the view point of size. To facilitate comparisons, totals for basal area are presented in terms of square feet per acre.

Density-Frequency-Dominance Index combines size, relative numbers, and distribution of individuals into a single expression giving an effective means of indicating relative importance for each species.

Synthetic Character

Presence and Constance: The usual five degree scale of presence and constance classes has been used to portray these useful characters of the abstract community.

Original Land Survey Interpretations

Interpretations of forest vegetation from the field

notes and maps of the original land survey (1837-1854) followed the method of Kenoyer (1929, 1934, 1939) in part. As an aid in making interpretations of plotted data, colored symbols were used for plotting witness and line trees from the field notes on the county map. Grouping ecological associations by means of colored symbols resulted in a pattern, when the map was completed, which was readily seen. This device reduced the time needed for interpretations considerably.

OBSERVATIONS AND RESULTS

UPLAND SECOND GROWTH HARDWOODS

The studies indicate that there is sufficient homogeneity to establish a typical grouping of species: *Acer saccharum-Fagus grandifolia* (Maple-Beech) association, although there is some variation between plots.

In describing the arborescent and shrubby vegetation in numerous stands of upland second growth hardwoods all of the species were listed and presence determined (Table 1). This procedure aided in determining species characteristic of the community and in formulating concepts with regard to uniformity and variations. Complete details of the species list may be found in Elliott (1952).

TABLE 1. Presence classes for the tree and shrub species in 98 stands of upland second growth hardwoods in Missaukee County, Michigan.

Canopy Trees	Percent	Class
Acer saccharum	95	5
Fagus grandifolia	86	5
Ulmus americana	57	3
Tilia americana	57	3
Fraxinus americana	43	3
Ulmus thomasi	35	2
Ulmus rubra	33	2
Prunus serotina	40	2
Acer rubrum	30	2
Tsuga canadensis	37	2
Betula lutea	19	1
Betula papyrifera	9	1
Quercus rubra borealis	15	1
Quercus alba	5	1
Pinus Strobus	5	1
Pinus resinosa	3	1
Thuja occidentalis	4	1
Fraxinus nigra	1	1
Understory Tree Species		
Ostrya virginiana	58	3
Prunus pensylvanica	41	3
Populus grandidentata	22	2
Populus tremuloides	3	1
Amelanchier sp.	8	1
Crataegus sp.	1	1
Shrubs		
Acer spicatum	4	1
Corylus cornuta	8	1
Cornus alternifolia	12	1
Ribes cynosbati	2	1
Rosa sp.	1	1
Sambucus pubens	3	1
Viburnum acerifolium	6	1
Spiraea sp.	1	1

Among canopy tree species, *Acer saccharum* and *Fagus grandifolia* are constantly present (93% and 86% respectively). Often present, when rated on the usual five degree scale of presence classes were: *Ulmus americana* 57%, *Tilia americana* 57%, and *Fraxinus americana* 43%. Other canopy tree species and their presence classes for the stands were: Class two (seldom present), *Prunus serotina* 40%, *Tsuga canadensis* 37%, *Ulmus thomasi* 35%, *U. rubra* 32%, *Acer rubrum* 30%. Class one (rare), *Betula lutea* 19%, *Quercus rubra* var. *borealis* 15%, *Betula papyrifera* 9%, *Pinus strobus* and *Quercus alba* 5%, *Thuja occidentalis* 4%, *Fraxinus nigra* 1%.

Ostrya virginiana (58%) and *Prunus pensylvanica* (41%) have the largest presence percentage (class three) for understory trees in the 98 stands, and only one understory tree (*Populus grandidentata* 28%) is in presence class two. Species in presence class one are: *Amelanchier* sp. 8%, and *Populus tremuloides* 3%.

The shrubby layer within the upland second growth hardwood stands includes 10 species. Each of these is only rarely present (class one). *Cornus alternifolia* is present most often, 12%; *Corylus cornuta* follows with 8% and *Viburnum* sp. and *Rhus typhina* are next with 6%. Species of *Sambucus*, *Ribes*, *Crataegus*, *Rosa* and *Spiraea* complete the list, all with a presence of less than 3%.

It is customary to name a vegetational community by its dominant species. Tables 2 and 3, in which the species are arranged in decreasing order of dominance as indicated by the DFD Index (Curtis 1947), shows that *Acer saccharum* is by far the most dominant species with a frequency of 94, a density

TABLE 2. Quantitative quadrat data for the tree species in upland second growth hardwoods in Missaukee County, Michigan. Based upon 546 quadrats in 98 stands. Frequency—% of total quadrats. Density—% of total (18460) stems in all quadrats. Basal area—% of total basal area (118.53 ft²/A).

Species	Frequency Percent	Density Percent	Basal Area Percent	DFD
Acer saccharum	94.14	60.59	35.83	1
Fagus grandifolia	50.73	8.04	12.67	2
Ulmus americana	32.78	3.76	12.92	3
Ulmus thomasi	22.53	3.96	10.89	4
Tilia americana	25.82	2.83	6.24	5
Ostrya virginiana	26.01	2.78	1.68	6
Fraxinus americana	19.05	1.99	2.97	7
Prunus pensylvanica	16.48	3.36	.25	8
Acer rubrum	13.19	3.90	2.16	9
Quercus rubra borealis	10.81	1.75	3.24	10
Populus grandidentata	10.44	2.49	2.15	11
Tsuga canadensis	11.72	.80	2.01	12
Prunus serotina	10.62	.72	2.46	13
Ulmus rubra	10.62	1.03	2.12	14
Betula lutea	5.68	.33	.54	15
Quercus alba	2.75	.55	.65	16
Betula papyrifera	2.93	.29	.36	17
Amelanchier sp.	1.65	.35	.03	18
Populus tremuloides	1.47	.20	.13	19
Pinus Strobus	1.28	.12	.32	20
Thuja occidentalis	1.28	.09	.16	21
Pinus resinosa	.55	.04	.12	22
Fraxinus nigra	.37	.03	.02	23

TABLE 3. Quantitative quadrat data for the tree species by size classes in 98 stands of upland second growth hardwoods in Missaukee County, Michigan.

Species	SIZE-CLASS TOTALS									
	2		3		4		5		6	
	Frequency Percent	Density Percent	Frequency Percent	Density Percent	Frequency Percent	Density Percent	Frequency Percent	Density Percent	Frequency Percent	Density Percent
Acer saccharum	76.92	66.64	86.80	65.74	73.63	45.78	29.99	14.93	6.23	29.20
Fagus grandifolia	27.11	7.94	26.01	7.57	24.36	6.87	17.40	16.07	4.76	19.71
Ulmus americana	7.69	2.17	11.90	2.90	21.06	6.29	13.37	15.65	3.48	14.60
Ulmus thomasi	6.78	2.02	11.36	3.14	17.58	7.65	10.44	14.82	1.65	12.41
Tilia americana	7.69	1.54	9.52	2.05	17.77	6.32	6.78	6.51	1.83	9.49
Ostrya virginiana	7.88	1.86	17.40	4.25	14.84	3.62	.91	.69		
Fraxinus americana	5.31	1.32	8.42	1.80	11.90	3.91	3.66	3.05		
Prunus pensylvanica	13.92	6.06	5.68	1.32	.37	.06				
Acer rubrum	8.24	3.54	9.34	4.74	8.24	4.35	1.28	1.11		
Quercus rubra v. borealis	3.85	.81	4.95	1.74	8.79	3.91	2.38	3.19	.36	2.19
Populus grandidentata	6.04	3.11	3.11	.87	7.33	3.33	2.93	2.35	.18	1.46
Tsuga canadensis	3.48	.79	2.38	.51	4.21	.90	2.02	1.66	1.28	4.38
Prunus serotina	1.65	.16	2.56	.47	6.41	1.62	4.58	4.71	2.02	3.65
Ulmus rubra	2.02	.68	4.21	.73	6.41	1.91	3.11	3.19	.37	1.46
Betula lutea	.55	.07	2.20	.36	4.21	.93	.55	.55		
Quercus alba	1.47	.45	1.65	.49	2.02	.90	.55	.55		
Betula papyrifera			2.02	.42	2.38	.99				
Amelanchier sp.	1.28	.48	.91	.38	.18	.03				
Populus tremuloides	.55	.16	.73	.30	.91	.23				
Pinus strobus	.73	.10	.18	.10	.18	.12	.37	.55	.18	.73
Thuja occidentalis	.18	.04	.73	.10	.73	.18	.18	.42		
Pinus resinosa	.37	.06			.18	.03			.18	.73
Fraxinus nigra			.18	.02	.37	.09				
		49.24		27.42		18.69		3.91		0.74

TABLE 4. Quantitative quadrat data for shrub species from 98 stands of upland second growth hardwoods in Missaukee County, Michigan. Frequency—% of total (546) quadrats; Density—% of total (592) shrubs.

Species	Frequency Percent	Density Percent	DF
Cornus alternifolia	4.95	44.34	1
Corylus cornuta	2.93	21.91	2
Viburnum acerifolium	1.65	10.10	3
Rhus typhina	1.28	7.19	4
Acer spicatum	1.10	6.14	5
Ribes cynosbati	.55	4.28	6
Sambucus pubens	.55	3.25	7
Crataegus sp.	.55	1.71	8
Rosa sp.	.18	1.20	9
Spiraea sp.	.18	.86	10

percentage of 61, and making up 36% of the total basal area. The tree species with second rank on the DFD Index is *Fagus grandifolia*: frequency 51; percentage of density 8; and percentage of basal area 13. Thus, the community may be characterized as an *Acer saccharum-Fagus grandifolia* association. The presence of *Tilia americana*, in all size classes, and of *Fraxinus americana* and *Betula lutea* in all but the largest size class is suggestive of the composition of northern hardwood deciduous forest communities. Representation of *Tsuga canadensis* and *Pinus strobus* in all five size classes, *Thuja occidentalis* in four of the five size classes, and *Pinus*

resinosa in three of the five size classes, adds the necessary elements to suggest a mixed conifer-northern hardwood forest community.

While there was no quantitative study made of the herbaceous vegetation because of the intense pasturing and frequent unselected cutting within the woodlots, the following species were noted during the study: *Allium tricoccum, Caulophyllum thalictaoides, Galium triflorum, Geranium robertianum, Hieracium aurantiacum, Hepatica acutiloba, Lycopodium complanatum, Mitchella repens, Osmorhiza claytoni, Polygonatum biflorum, Oxalis acetosella, Pteridium aquilinum, Thalictrum dioicum, Solidago* sp., *Trillium grandiflorum, Viola pensylvanica, V. pubescens,* and *V. canadensis.*

UPLAND SECOND GROWTH HARDWOODS IN RELATION TO THE SIX SOIL SERIES

Acer saccharum is the dominant canopy tree species on all soils except Roselawn (Fig. 2), which supported Norway pine, white pine and oaks in its virgin condition (Veatch 1943). After lumbering and subsequent fires, the coniferous element has all but disappeared and deciduous trees such as *Quercus rubra* var. *borealis, Acer rubrum, Quercus alba* and *Acer saccharum* form the arborescent layer of the second growth forest. Quantitative data for the 23 quadrats on Roselawn soils (Table 5) indicate that the forest may be considered as a *Quercus rubra* var. *borealis-Acer rubrum* lociation within the *Acer saccharum-*

Fagus grandifolia association. On the basis of size class representation for the 16 tree species recorded on this soil series, those of size class two are dominant, composing 55% of the total. Those trees of size class three made up 27% of the total; size class four, 15%; size class five, 2%; and size class six, .11%.

TABLE 5. Quantitative quadrat data for tree species of upland second growth hardwoods located on the Roselawn soil series. Density in % of total (938) stems; basal area in % of total (88.01) ft²/A.

Species	Frequency Percent	Density Percent	Basal Area Percent	DFD
Quercus rubra v. borealis....	95.65	18.87	55.80	1
Acer rubrum...............	69.75	30.59	4.91	2
Quercus alba..............	47.83	10.02	16.70	3
Acer saccharum...........	30.43	19.40	3.44	4
Fagus grandifolia.........	21.74	8.31	.93	5
Prunus pensylvanica.......	21.74	2.88	.32	6
Tilia americana............	13.04	1.17	6.38	7
Pinus Strobus.............	13.04	.96	4.44	8
Populus grandidentata......	13.04	4.00	2.49	9
Ostrya virginiana..........	13.04	1.39	.77	10
Pinus resinosa............	8.70	.62	.32	11
Ulmus americana..........	4.35	.43	1.99	12
Prunus serotina...........	4.35	.32	.91	13
Ulmus rubra..............	4.35	.32	.44	14
Amelanchier sp............	4.35	.43	...	15
Fraxinus americana........	4.35	.11	.16	16

Pinus strobus (DFD-8) and *P. resinosa,* (DFD-11) indicate the present ranking of the coniferous element for the Roselawn soil series.

On soils where *Acer saccharum* dominated, lower ranking societies were not always similar in composition. On Arenac an *Acer saccharum-Ulmus thomasi* lociation occurs (Table 6). Sugar maple is the only species on this soil represented in all size classes. Both *Ulmus thomasi* and *Fagus grandifolia* are in the first four size classes, while *Ulmus americana* is absent in both size class two and six. The coniferous element is represented by a lone relic species of *Tsuga canadensis,* in size class six.

TABLE 6. Quantitative quadrat data for tree species of upland second growth hardwoods located on the Arenac soil series. Density in % of total (473) stems; basal area in % of total (142.13) ft²/A.

Species	Frequency Percent	Density Percent	Basal Area Percent	DFD
Acer saccharum............	100.00	66.81	33.76	1
Ulmus thomasi.............	42.11	11.63	11.36	2
Ulmus americana..........	36.84	6.13	21.50	3
Fagus grandifolia..........	31.58	3.38	10.83	4
Ostrya virginiana..........	36.84	3.38	1.93	5
Fraxinus americana........	21.05	.85	3.07	6
Tilia americana............	15.79	2.54	4.07	7
Prunus pensylvanica........	10.53	2.11	....	8
Acer rubrum..............	10.53	1.90	.14	9
Tsuga canadensis..........	5.26	.21	2.70	10
Quercus rubra v. borealis....	5.26	.85	1.04	11
Prunus serotina.	5.26	.21	1.13	12

FIG. 3. Upland second growth hardwood on Arenac soil with *Ulmus thomasi* prominent in the foreground, *Acer saccharum* the other dominant.

Ostrya virginiana is the dominant understory species and *Prunus pensylvanica* the only associate. Shrubs are absent on the quadrats studied.

Thirty-seven percent of the tree species on Arenac are in size class two; 31% in size class three; 24% in class four; 7% in class five; and 0.5% in size class six.

Nineteen tree species were recorded on Emmet soil quadrats (Table 7). Of the 11,918 trees measured, 52% are in size class two; 29% in size class three; 16% in size class four; 3% in size class five; and 0.5% in size class six.

FIG. 2. Second growth upland hardwood on Roselawn soil series—west facing morainic slope. Northern red oak-red maple the dominants.

TABLE 7. Quantitative quadrat data for tree species of upland second growth hardwoods located on the Emmet soil series. Density in % of total (11918) stems; basal area in % of total (104.2) ft² /A.

Species	Frequency Percent	Density Percent	Basal Area Percent	DFD
Acer saccharum............	£8.70	67.16	39.00	1
Fagus grandifolia.........	54.30	8.80	14.00	2
Ulmus americana..........	38.80	4.07	16.00	3
Tilia americana..........	31.30	3.29	7.00	4
Ostrya virginiana...........	21.10	2.92	2.00	5
Frazinus americana........	20.10	2.22	3.00	6
Prunus pensylvanica.......	19.20	2.75	.50	7
Ulmus thomasi............	12.10	1.98	7.00	8
Populus grandidentata.....	10.80	2.11	2.00	9
Prunus serotina...........	9.69	.60	3.00	10
Ulmus rubra..............	9.20	.84	2.00	11
Quercus rubra v. borealis....	9.00	.94	2.00	12
Acer rubrum..............	8.00	1.38	1.00	13
Tsuga canadensis..........	6.50	.23	1.00	14
Betula lutea..............	3.70	.19	.50	15
Populus tremuloides........	1.50	.26	....	16
Amelanchier sp.............	1.50	.17	....	17
Quercus alba..............	.90	.03	....	18
Betula papyrifera..........	.60	.03	....	19

FIG. 4. Second growth hardwoods on Emmet soil—east facing morainic slope. Sugar maple and beech dominant.

In addition to *Acer saccharum* and *Fagus grandifolia*, other canopy tree species with high DFD Index values are: *Ulmus americana* (3); *Tilia americana* (4); *Fraxinus americana* (6); and *Ulmus thomasi*

(8). Three understory tree species which rank high on the DFD Index are: *Ostrya virginiana* (5); *Prunus pensylvanica* (7); and *Populus grandidentata* (9). As was the case on Arenac, the only representative of the conifers is *Tsuga canadensis*. However, unlike the situation on Arenac soils, it was represented in all five size classes. The shrubby layer of vegetation is composed of 8 species with *Cornus alternifolia* being the most abundant.

The quantitative data for Kalkaska quadrats (Table 8) indicate an *Acer saccharum-Ulmus tho-*

TABLE 8. Quantitative quadrat data for tree species of upland second growth hardwoods on the Kalkaska soil series. Density in % of total (725) stems; basal area in % of total (153.5) ft² /A.

Species	Frequency Percent	Density Percent	Basal Area Percent	DFD
Acer saccharum............	100.00	75.44	45.6	1
Ulmus thomasi.............	55.17	9.66	26.6	2
Fagus grandifolia..........	51.72	6.07	12.2	3
Ostrya virginiana..........	34.48	2.34	1.2	4
Ulmus americana..........	17.25	3.03	2.0	5
Prunus serotina............	24.14	1.10	1.9	6
Tilia americana............	10.34	.69	3.0	7
Prunus pensylvanica	3.44	.97	...	8
Tsuga canadensis..........	3.44	.14	.3	9
Populus grandidentata......	3.44	.14	.2	10
Frazinus americana........	3.44	.28	...	11
Ulmus rubra..............	3.44	.14	...	12

FIG. 5. Upland second growth hardwoods on Kalkaska soil—till plain. Sugar maple-elm lociation.

masi lociation. Other canopy tree species and their order of dominance as indicated by the DFD Index are: *Fagus grandifolia* (3); *Ulmus americana* (5);

TABLE 9. Quantitative quadrat data for tree species of upland second growth hardwoods on the Nester soil series. Density in % of total (2412) stems; basal area in % of total (113.7) ft²/A.

Species	Frequency Percent	Density Percent	Basal Area Percent	DFD
Acer saccharum	93.60	48.05	33.82	1
Fagus grandifolia	49.30	6.51	7.90	2
Ulmus americana	32.90	3.94	8.29	3
Ostrya virginiana	34.10	3.68	3.28	4
Ulmus thomasi	25.10	4.27	11.37	5
Tilia americana	29.10	2.36	6.80	6
Tsuga canadensis	27.80	1.82	4.59	7
Populus grandidentata	18.90	6.43	4.79	8
Fraxinus americana	20.20	2.57	5.26	9
Prunus pensylvanica	16.40	7.55	....	10
Prunus serotina	18.90	1.45	3.00	11
Acer rubrum	12.60	4.89	4.33	12
Ulmus rubra	15.00	.62	1.19	13
Betula papyrifera	11.40	1.58	1.61	14
Betula lutea	12.60	.62	.48	15
Thuja occidentalis	4.90	.49	.85	16
Pinus Strobus	3.50	.37	1.23	17
Populus tremuloides	3.50	.91	.50	18
Amelanchier sp.	3.50	1.20	.03	19
Quercus' ubra v. borealis	3.50	.49	.44	20
Fraxinus nigra	2.00	.17	.22	21

Prunus serotina (6); *Tilia americana* (7); *Tsuga canadensis* (9); and *Fraxinus americana* (11). Hemlock is the only coniferous element. The percentage of trees in the various size classes recorded on the Kalkaska complex follows: Size class two 42%; size class three 25%; size class four 23%; size class five 7%; size class six 3%. *Ostrya virginiana* (DFD-4) is the abundant tree of the understory. Two other tree species: *Prunus pensylvanica* (DFD-8) and *Populus grandidentata* (DFD-10) complete the understory layer. The quadrats are devoid of shrubs.

There are 19 species of trees recorded on Nester quadrats (Table 9). *Acer saccharum* and *Fagus grandifolia* are the two dominant tree species of the forest canopy. Other canopy tree species attaining high values on the DFD Index are: *Ulmus americana* (3); *Ulmus thomasi* (5); *Tilia americana* (6); and *Tsuga canadensis* (7). Forty-five percent of all trees on this soil series are in size class two; 24% in size class three; 25% in size class four; 5% in size class five; and 0.5% in size class six.

Presence of *Pinus strobus, Tsuga canadensis* and *Thuja occidentalis* here is suggestive of the character of a mixed conifer-northern hardwood community. Five tree species make up the understory with *Ostrya virginiana* most abundant. Eight shrubby species occur.

There is an *Acer saccharum-Ulmus thomasi* locia-

FIG. 6. Second growth hardwoods on Nester soil with *Betula lutea* prominent in the foreground but sugar maple-beech dominant.

FIG. 7. Upland second growth hardwoods on Selkirk soil—till plain. Sugar maple-elm dominant.

tion on the Selkirk soils (Table 10), where 42% of the trees were in size class two; 24% size class three; 25% size class four; 7% size class five; and 2% size class six.

A comparison of the composition of the vegetation on the six soil series shows that there are three edaphic lociations making up the Maple-Beech association. Emmet and Nester soils have a typical *Acer saccharum-Fagus grandifolia* association, Roselawn has a *Quercus rubra* var. *borealis-Acer rubrum* lociation, whereas Arenac, Kalkaska and Selkirk have an *Acer saccharum-Ulmus thomasi* lociation. These various lociations, are probably representative of stages of succession.

Forest Distribution as Interpreted From the

Original Land Survey (1837-1854)

The forest vegetation, as interpreted from the field notes and maps of the original land survey, was a typical Hemlock-Hardwoods association (Oosting 1948, p. 250). The forest may be divided into four communities: swamp, pine, mixed conifer-northern hardwood, and hardwood (Fig. 8).
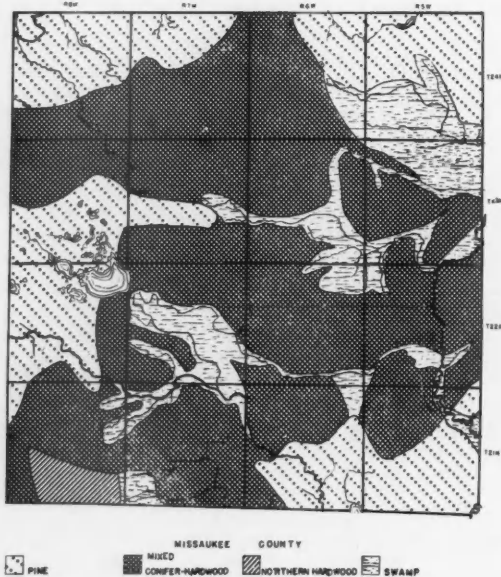

FIG. 8. Map of Missaukee County showing the distribution of the original forests as interpreted from the original land survey, 1837-1854.

Prior to plotting data from the surveyor's field notes upon a county map, a list of 33 different common names for the tree species was compiled. There is good possibility that some of these common names represent duplications of the same species, especially among the pines. However, as only common names were used by the surveyors, it was impossible to ascertain all possible duplications. Beal (1888, p. 79) has given some indication of possible duplication of names among the pines:

. . .The botanist will tell you that in Michigan, there are three and only three species of pine, while the lumberman says there are eight or ten. He applies the term "buckwheat pine" to a thrifty, usually young tree of white pine which has a large, low top.—Occasionally some call a tree of *Pinus Banksiana*, "buckwheat pine" if it has the shape above described.

. . ."Sapling" or "Bull sapling," is the name applied to a tall and thrifty white pine with a good top.

. . .The red or "Norway pine" (lumberman universally call it by the latter name) is called "black Norway" when the trees are low and have large tops and a relatively large proportion of sap wood. A tree is "yellow Norway" when it is tall with a small top, when it is making a slow growth and has but little sap wood.

. . .Where trees of *Pinus Banksiana* are short, with large, wide tops, and the proportion of sap wood large, they are called "black jack pine." Where they are crowded, tall, with small tops and a large proportion of heart wood, they are called "yellow jack pine."

In making comparisons between the forests as interpreted from the original land survey, and the present day composition of upland second growth hardwood communities as determined by quadrat studies, it was necessary to make some interpretations regarding possible duplication of names of the tree species as used by the surveyors and in this study. Here, the number of individuals recorded by the surveyors as either red or Norway pine are considered together as a single species, *Pinus resinosa*. It will be noted in the statement of Beal (1888), quoted above, that "yellow" pine of the surveyors might be either *Pinus banksiana* or *P. resinosa*. Because of the habitat where this species was most frequently noted by the surveyors, it is presumed that "yellow" pine, as used by the surveyors in Missaukee County, referred to *P. resinosa*. However, as it was impossible to establish exact duplication in this instance, trees recorded as "yellow" pine are not included in the tabulation for *P. resinosa*, but appear within the tables as "yellow" pine. The list of common names, as used by the surveyors, contains three representatives of Acer: "Maple," Red Maple, and "Sugar." The latter is a term used frequently in identifying both witness and line trees in the field notes. It is here interpreted to mean *Acer saccharum*. "Maple," as used by the surveyors, is interpreted to mean any other species of Acer. In the computations made, the number of individuals recordered as either "Maple" or Red Maple are grouped together as a single total under *Acer rubrum*. There were three different oaks referred to by the surveyors: Red, White, and "Black." These have been treated as three separate species but there is some question as to the identity of the "Black" Oak of the surveyors. In many instances, present land owners, when speaking about their woodlots, frequently used the term "Red-Black" Oak. This practice could possibly be interpreted to indicate that the "Black" Oak of the surveyors is the "Red-Black" Oak of the present land owner, which is *Quercus rubra* var. *borealis* of

this study. Both *Populus grandidentata* and *P. tremuloides* appear in the quantitative data of the present day study. Surveyor's field notes contain only the common name Aspen. When contrasting the vegetation of the two periods of time, the surveyor's Aspen has been considered as comparable to *Populus grandidentata* of today as the habitat in which the Aspen was noted by the surveyors was typical of *P. grandidentata* rather than of *P. tremuloides*.

Kinds of quantitative expressions which might be used for indicating phytosociological aspects of forest distribution as interpreted from the original land survey are of necessity limited to the restricted data of the field notes. Yet, as Blewett & Potzger (1950) have said:

> It is very likely that a few representatives of a mass of vegetation taken at widely separated points within a large area give the same picture as does a concentrated tabulation of a small area. We find this to be true of other situations.

The operation of this "law" is assumed in this situation. Two phytosociological criteria have been used in making an interpretation of the forest composition from the data of the original land survey field notes. One, constance, is a synthetic character which treats of the community in the abstract; the other, density, is a quantitative character showing structural characteristics of the concrete community.

In this instance, the county has been considered the extent of the community, and specific township sections were chosen to represent the unit areas from which the synthetic character of constance was obtained. Sections 8, 11, 26, and 29 within each of the 16 townships were selected. This selection gave a wide and even distribution and avoided duplications

TABLE 10. Quantitative quadrat data for tree species of upland second growth hardwoods on the Selkirk soil series. Density in % of total (2007) stems; basal area in % of total (164.2) ft²/A.

Species	Frequency Percent	Density Percent	Basal Area Percent	DFD
Acer saccharum	93.06	48.63	34.50	1
Ulmus thomasi	55.56	13.30	16.63	2
Fagus grandifolia	52.78	7.03	12.97	3
Acer rubrum	25.00	7.08	5.06	4
Tsuga canadensis	26.39	3.64	3.73	5
Ulmus americana	20.83	2.99	7.05	6
Fraxinus americana	23.61	1.69	3.03	7
Ostrya virginiana	22.22	1.54	.90	8
Ulmus rubra	16.67	3.49	3.09	9
Tilia americana	11.12	2.24	5.64	10
Prunus serotina	13.89	.75	1.85	11
Betula lutea	12.50	1.10	1.07	12
Prunus pensylvanica	9.72	3.29	....	13
Betula papyrifera	6.94	.65	.51	14
Quercus rubra v. *borealis*	5.56	.90	1.16	15
Populus grandidentata	4.17	.65	1.82	16
Thuja occidentalis	4.17	.25	.24	17
Amelanchier sp.	2.79	.50	....	18
Pinus resinosa	1.39	.05	.57	19
Quercus alba	1.39	.15	.18	20
Pinus Strobus	1.39	.10	....	21

TABLE 11. Constance and constance classes as compiled from field notes of the original land survey.

Species	Percent	Class
Alder	1	1
Ash, Black	37	2
Ash, White	1	1
Aspen	8	1
Basswood	8	1
Beech	85	5
Birch, White	12	1
Birch, Yellow	37	2
Cedar	37	2
Cherry, Black	6	1
Dogwood	3	1
Elm	28	2
Fir	22	2
Hemlock	95	5
Ironwood	8	1
"Maple"	73	4
Oak, "Black"	6	1
Oak, Red	17	1
Oak, White	6	1
Pine, Jack	1	1
Pine, Norway	19	1
Pine, "S"	1	1
Pine, White	82	5
Pine, "Yellow"	26	2
Spruce	4	1
Spruce, Black	17	1
"Sugar"	69	4
Tamarack	32	2

of data by eliminating any joint section boundaries. Constance, expressed in a five degree scale of classes, indicates a forest at the time of the original land survey fitting the present concept of the Hemlock-Hardwoods association (Table 11). Hemlock was an important and constantly present member (class 5) of the community, as were beech and white pine. Both "Sugar" (*Acer saccharum*) and "Maple" attained fourth class ranking (mostly present). None of the 28 species could be given third class ranking; however, 7 species could be considered as seldom present on the basis of class two ranking. The remaining species all belonged to class one.

Density (% of total) was obtained for the concrete stand by counting all of the recorded trees in the same sections as used in obtaining constance. There was a total of 2,038 trees listed by the surveyors in sections 8, 11, 26, and 29 of all townships. Totals for the different species divided by the sum total of all trees gave an expression of percent density for each kind of tree (Table 12). The species having the highest percent density (23%) was hemlock; beech was second highest (19%); "Sugar" (12%) was third and white pine (11%) was fourth.

SWAMP COMMUNITIES

The swamp communities were located along the numerous streams and were, for the most part, on till plains and outwash aprons. According to the field notes many of these areas were characterized as "variety" swamps. Woody vegetation of such areas, as noted by the surveyors, included alder, cedar, hemlock, aspen, black spruce, tamarack, black ash and willow. In other swampy areas the vegeta-

TABLE 12. Percent density based on total (2038)
stems of the tree species as compiled from the data of
the field notes of the original land survey for sections
8, 11, 26 and 29 of each township in the county.

Species	Percent Density
Hemlock	22.90
Beech	19.33
"Sugar"	11.56
White Pine	11.29
"Yellow" Pine	5.85
Norway Pine	4.40
"Maple"	4.35
Cedar	4.25
Tamarack	3.30
Black Ash	2.30
Yellow Birch	1.60
Elm	1.40
Fir	1.30
"S" Pine	1.24
Black Spruce	1.23
White Birch	.59
Red Oak	.54
Aspen	.49
"Black" Oak	.44
Ironwood	.44
Basswood	.25
Black Cherry	.25
White Ash	.20
White Oak	.20
Dogwood	.10
Spruce	.10
Jack Pine	.05
Alder	.05

tion was apparently less varied as the surveyors dis-
tinguished them by such phrases as: "alder thicket;
tamarack, cedar, hemlock swamp; cranberry swamp;
black ash thicket; tamarack, cedar, spruce, swamp."

PINE COMMUNITIES

Fig. 8 shows that the pine communities occupied
four areas at the time of the original land survey.
The southeast, northeast, and northwest corners and
the lake area in the west central portion of the
county were covered with "pine plains." Topograph-
ically, the limits of the pine communities do not
correlate with any one physiographic feature but
rather embrace all three forms, However, compar-
ison of the limits of distribution for these pine
communities with an unpublished land type map
(Veatch 1942) indicates that they are situated in
areas of sandy soil.

To obtain some expression of the degree of domi-
nance for the various trees within one of the pine
communities, the total number of listed trees was
determined and percent density was calculated for
the individual species. On the basis of these data
(Elliott 1952), white pine could be considered the
dominant species with "yellow" pine, hemlock and
Norway pine the principal secondary dominants.

The quadrat studies on the Roselawn complex were
located within the limits of this pine community as
indicated by the survey records. The present forest
community has been shown to be of a deciduous
character with *Quercus rubra* var. *borealis* dominant.
Present representatives of species which gave charac-

ter to the former pine community are two in number:
Pinus resinosa and *P. strobus*. Percent density for
Pinus resinosa, as calculated from data derived from
the original survey, is 11. Percent density for this
species in the quadrat studies is .62. *Pinus strobus*
has a percent density of 28 within the pine commu-
nity of the original land survey. Percent density for
the species in quadrats on Roselawn soils is .96.

Diameter sizes for the trees, as entered in the field
notes, indicate that the trees used as reference
points were large ones, for the most part. The
range of diameters varies from 8 to 52 in., the
latter a white pine. The record for diameters of the
present day coniferous representatives of this former
pine community is somewhat different. One of the
nine individuals of white pine now present belonged
to size class six, having a diameter of 15.6 inches,
which is the lowest limit for the size class. It
could be interpreted from these data (Elliott 1952)
that the two white pines of the largest size classes
(size class six and five) are relics of the former pine
community and that the seven specimens in the small-
est size class (size class two) are indicative of suc-
cessful reestablishment following lumbering and fire.
Yet, occurrence of white pine in all size classes today
is insignificant when compared with only the larger
individuals used as reference points by the survey-
ors.

THE MIXED CONIFER-NORTHERN HARDWOOD COMMUNITY

The most extensive community at the time of the
original land survey was the mixed conifer-northern
hardwood community (Fig. 8). This expression of
the forest community occupied more than half of the
area of the county. The data, as compiled from the
field notes, indicate that at times the conifers and
northern hardwoods formed extensive tracts of forest
of a mixed character, while at other times, now one
and then the other was more abundant in occurence,
resulting in small islands of either hardwoods or
conifers surrounded by the larger mixed forest com-
munity. Beech, "sugar," "maple," white pine, hem-
lock, Norway pine, basswood, black cherry, red oak,
jack pine, white and "black" oak were frequently used
as witness and line trees by the surveyors within the
limits of distribution of these communities.

So as to have some basis for quantitative com-
parison between the mixed conifer-northern hardwood
community at the time of the original land survey
and the present composition of the same region, as
indicated by this study, two areas located within the
original land survey were arbitrarily selected and
percent density for the recorded trees was calculated.
The arbitrary selections were made from the map
constructed from the original field notes, which
showed, by symbols, the species used as reference
points for the witness and line trees. Selections were
made to give two varied expressions representative
of the community: one area gave the appearance
of having an abundance of hardwood species and
the other appeared on the map as having a more

even mixture of conifers and northern hardwoods. The first area comprised sections 31, 32, 33, 34 and 35 of T24N: R7W and sections 1, 2, 3, 4, 5, and 6 of T23N: R7W. The number of trees recorded in the field notes for this area was 222. Nine species were used by the surveyors as witness and line trees. On the basis of percent density as a criterion for dominance, this area could be characterized as a Beech-Hemlock-Maple association. Beech (108 trees) had a percent density of 49; hemlock (53 trees) had a percent density of 24 and "sugar" (49 trees) 22%.

Except for a small area of swamp land in the southern part of T24N: R7W, section 34 and T23N: R7W, section 3, the area under consideration lies entirely within the Emmet complex of this study. Quadrat studies here showed that the present community is a Maple-Beech association. Hemlock is still a constituent of the forest community, but it no longer plays a prominent part, being ranked 14th on the DFD Index, which included 19 species. The second area selected as a basis for comparison with the present quadrat studies was composed of sections 1-5; 8-12; 13-17 of T22N: R7W. Two hundred sixty four individuals, representing 14 species, 4 of which were conifers, were listed for the area. Whereas the same species had the highest percentage of density originally and today, the data for the remaining species indicate a greater mixture of conifers and northern hardwoods within the area at the time of the original land survey.

Quadrat studies of the present forest composition within this area include stands on Arenae, Emmet and Selkirk soils. *Acer saccharum* and *Fagus grandifolia* are co-dominant with hemlock, and white and Norway pine are never significant.

THE HARDWOOD COMMUNITY

A small portion of the southeastern part of T21N: R8W supported a northern hardwood community, according to the data compiled from the field notes. Brink's (1837) description of the area stated, in part:

. . .There is a great majority of the timber in the southern part of the township of the finest and largest sugar trees that I have seen affording a great opportunity of making sugar. The trees have never been tapped or worked.

The area is confined to the massive moraine of the Lake Michigan-Saginaw Interlobate Tract (Leverett 1924). In the field notes 267 trees of 12 species are mentioned. On the basis of percent density as a criterion for dominance, "sugar" was dominant (56%) and beech next (22%). This hardwood community is represented in the quadrat studies by the Emmet complex. Data of this study indicate that "sugar" (*Acer saccharum*) and beech (*Fagus grandifolia*) are the dominant tree species and that the status of many of the other deciduous species is similar. Hemlock, while still present today, is less plentiful, and white pine, present in the community at the time of the original survey, does not appear.

DISCUSSION

THE UPLAND SECOND GROWTH HARDWOOD

The dominant plants of any community are considered to be those which, by reason of their size, abundance and distribution, largely determine the conditions under which other organisms live in association with them, On the basis of these criteria of dominance, *Acer saccharum* far surpasses any other species.

According to Braun (1950, p. 352): "All statistical data for the hardwood forests of this part of the section (Northern lower Michigan) illustrate the overwhelming dominance of sugar maple and beech, not only in the forest canopy, but in the lower layers as well." Whereas this study bears out the above statement regarding sugar maple, the data indicate that beech is less dominant. It should be pointed out that, while the quantitative data represent *Fagus grandifolia* as being considerably less dominant than *Acer saccharum*, certain disturbance factors have been responsible for producing some of these differences. Land owners reported that during World War II, there was considerable selective cutting of beech within the county to satisfy the demands of the aircraft industry. The many beech stumps within the woodlots are supporting evidence. However, the amount of beech taken out at that time, as indicated by the stumps, does not begin to account for the loss in dominance of Fagus in the community between the time of the original land survey and this study. The cultural practice of using all woodlots for open pasture has also been responsible for some lessening in the abundance of the species. While sugar maple is the most aggressive reproducer, beech, which is probably more tolerant, does not usually bear as large an annual seed crop, and much of that which is borne may be destroyed by animals. Thus, while *Fagus grandifolia* was more abundant before settlement, its numbers are less today because of selective cutting and pasturing.

On the basis of the DFD Index, *Ulmus americana* ranks third. However, greater reproduction of *U. thomasi* than of *U. americana* in size class two (Table 3), suggests the close relationship of these two species within the community.

Alone or together, the three species of Ulmus are an important part of the composition of stands of upland second growth hardwoods. They occur on outwash aprons and till plains as well as on the crests and slopes of moraines. Ulmus is a constant associate in the community. On all these varied sites where the three species were found during this study in Missaukee County, they appeared to have become successfully established. On the basis of high percentages of frequency, density and basal area, it would further appear that Ulmus plays a more important role in the composition here than is usually considered. Frothingham (1915) credited elm with comprising 8% of the forest cover of the state. However, in describing the composition of northern hardwoods in Michigan and Wisconsin he said: "Basswood

and elm sometimes form one third of the total stand."
Potzger (1946) indicated an abundance percentage of
3 for Ulmus in a transect across eastern Wisconsin
and upper and western lower Michigan. Braun
(1950, p. 353) in a study of two hardwood stands
in northern lower Michigan, indicated that *Ulmus
americana* made up 3.2% of the forest at Mud Lake
on mucky soils of shallow ravines and only 0.3% of
the canopy forest on better drained soils of swells.
In the second layer, *Ulmus americana* had a percent-
age of 7.7 on the former soil and 1.3% on the latter.
Her figures for a hardwood stand at Carp Lake in-
dicate a percentage of 0.4 for *U. americana* in the
forest canopy on an old beach ridge and no data for
the second layer. The typical beech-maple forest at
Carp Lake (p. 353) includes no *Ulmus thomasi* or
U. rubra in either the canopy or second layer.

Dansereau (1946), Blewett & Potzger (1950) and
Braun (1950) indicated that Ulmus is successional in
the northern hardwood forest area. Dansereau's
(1946, p. 240) "Quasi climax" contains one element
which he characterizes as the "Aceretum saccharo-
phori ulmosum." It precedes the climax "Aceretum
saccharophori laurentianum." Preceding the "Quasi
climax," there is a segment indentified as the "Acere-
to-Ulmetum laurentianum," which is an earlier suc-
cessional stage, called by Dansereau "The Sous-Cli-
max" (sub-climax). Braun (1950, p. 356) presents
a successional diagram showing the various forest
communities as related to one another in the sequence
of decreasing water requirements. In the diagram
sugar maple-beech is at the top and a complex of
sugar maple, basswood, elm, and beech is next in
order.

On the other hand Frothingham (1915), Quick
(1923), Gleason (1924), and Nichols (1935) con-
sidered *Ulmus americana* to be a climax dominant
in mixed conifer-northern hardwood forests. Quick
(1923, p. 224) stated that: "*Ulmus americana*, the
white elm, is a member of the climax association
throughout the Lower Peninsula, especially in the
southern part. Its ratio of occurrence on sand and
clay is 3:5. Next to the sugar maple it is the most
common member of this association." Gleason (1924)
said that there are 23 species characteristic of this
association which is distinguished not only by the
wide distribution of the species, but also by their
high frequency indices within the area. American
elm is one of the species making up this list. In
describing the Hemlock-White Pine-Northern Hard-
wood Region of Eastern North America, Nichols
(1935, p. 408) stated that basswood and elm, though
sparingly represented in the climax forest eastward,
are much more extensively developed westward where,
"in the Lake States the two together comprise more
than 20% of the hardwoods." It is the writer's
opinion that the first view (Ulmus as a subclimax,
successional species) leads naturally into the latter
one. Apparently the elms are more abundant, and
hence attain greater dominance, in the late stages of
the subclimax, but they remain as components of
the climax forest although reduced in abundance.

The elms are less tolerant than either sugar maple
or beech (Frothingham 1915, p. 16). Consequently,
they could attain better status under the more open
conditions of the forest canopy during the subclimax
stage than they would when sugar maple and beech
produce a dense shade. This may account for the
position of dominance attained by both *Ulmus ameri-
cana* and *U. thomasi* in the present stands of upland
second growth hardwoods in Missaukee County,
Michigan.

Assuming that normal successional patterns will
remain in force within the hardwood stands of the
county, it may be expected that the elms will drop
out of their present dominant place in the community.
Normal succession should result in a Maple-Beech
canopy sufficiently dense to reduce considerably the
less tolerant elms within the stands. However, pres-
ent cultural practices, now operating as disturbance
factors should retard the normal course of succession
for some time to come.

The county is just north of the reported northern
limits of distribution for *Ulmus thomasi* (Harlow
& Harrar 1950, p. 386; Little 1949, p. 787; Hough
1947, p. 184; Dominion Forest Service 1949, p. 186).
The nearness of the county to the northern limits of
the range for this species should result in critical
growth conditions for this tree (Cain 1944, p. 19).
However, quadrat data (Table 3) indicate that such
is not the case here. Operation of certain compen-
sating factors, such as microclimates, genetics and
edaphics often permits disjunets to grow at the edge
of their range without adverse effects. Yet the vari-
ety of sites on which this species was found, as
well as its great abundance, suggest a northward
extension of its range.

Earlier literature on the maple-beech association
and the mixed conifer-northern hardwood forest com-
munity as they occurred in Michigan (Quick 1923;
Gleason 1924; Gates 1912, 1926; Woollett & Sigler
1928) indicated that hemlock (*Tsuga canadensis*),
occurring within the forest community, should be
interpreted as a relic. Gleason (1924, p. 294) stated:

. . . Hemlock is present . . . but hemlock seedlings were
not observed. Almost all hemlock in the hardwood
stands of the region were veterans. After their death,
which may be expected in a comparatively short time,
hemlock will practically disappear as a component of
the association.

Yet, today, hemlock has a presence class of two
(seldom present), instead of class one (rare). On
the DFD Index it ranks 12th (Table 2). The
species was present in every size class (Table 3)
indicating that it was a successful member of the
community. Other coniferous representatives, which
gave character to the mixed conifer-northern hard-
wood community of the primeval forest, are sadly
depleted (Tables 2, 3).

Yellow birch (*Betula lutea*) is a characteristic
species of the northern hardwood forest community.
Within the upland second growth hardwoods under
study, it is today only rarely present (Table 1).

According to the DFD Index (Table 2) it ranks 15th in importance among the total of 23 tree species. The birch is represented in all but the largest size class and is most frequent in size class four. Basswood (*Tilia americana*) is also a characteristic species of the northern hardwood forest community. In this study the species ranked fifth on the DFD Index. Like the elms, its density is greatest in the larger size classes and the relative percent of frequency about the same throughout all five size classes.

The present ecological status of *Acer saccharum* in the community cannot be questioned. The ecological role of *Fagus grandifolia, Ulmus americana, U. thomasi, Tilia americana, Betula lutea* and *Tsuga canadensis* has been discussed in detail. These species are considered as representatives of the mature (climax) forests of the area. That the present upland second growth hardwood stands are not climax is attested by the presence of such subclimax species as *Betula papyrifera, Quercus rubra* var. *borealis,* aspen and fire cherry. The quantitative data indicate that the composition of these stands fits nearest Type 12 (Sugar Maple-Beech-Yellow Birch) of the forest cover types given by the Society of Foresters for the eastern United States (1932, p. 463).

Only 1.05% of the individuals included in this study were coniferous. This small amount could not be considered of enough importance to give character to the forest. Thus, it would be improper to consider these stands as representative of a mixed conifer-northern hardwood community. Rather, the conifers are better considered as relics of an association typical of this area at an earlier date.

More than 50 years ago Whitford (1901) traced the life-history of the vegetation of 4 physiographic formations in northern Michigan and found "that in each series the climax plant growth is a deciduous-hemlock combination." His tentative conclusion, after considering the whole region from an ecological standpoint, was that the vegetation:

... cannot reach maturity until it does so physiographically. Thus the development of the forest is held back until the normal physiographic processes extinguish the swamps and lakes. When these are eliminated, the region will reach old age from the vegetation standpoint much sooner than it does physiographically, because the climate is favorable for the extension of mesophytic forests into altitudes which would otherwise support only a xerophytic society.

The data (Tables 2, 3) appear to substantiate his conclusion regarding the vegetation. Wide distribution of maple-beech communities on varied physiographic sites throughout the county and establishment of a *Quercus rubra* var. *borealis-Acer rubrum* lociation, or of aspen associations where pine formerly grew, are evidence in support of Whitford's conclusion. Further, reduction in size of areas now occupied by swamp communities indicates physiological ageing.

Quick (1923) said that the whole lower peninsula of Michigan would support a maple-beech association

when the time factor was sufficiently long enough to allow for the establishment of association dominants in all areas. Present data likewise appear to support this contention.

It is probable that the previous mixed conifer-northern hardwood aspect of the forest was the result of the "lagging" of coniferous species. Almost total destruction of this element as a result of logging and subsequent fires during the latter half of the 19th century resulted in elimination of these relic species from the community and the reestablished forests are developing towards the true climax. All evidence suggests that the northern portion of Michigan's lower peninsula should not be considered as a part of the mixed conifer-northern hardwood forest of eastern North America but that coniferous species play a relic role in a deciduous forest community as climax.

There has developed, over the years, a theory of a warming climate, especially on the North American continent. Evidence in support of this theory continues to accumulate with increasing literature from a variety of sources. Veatch (1937) presented pedologic evidence of changes in climate in Michigan in support of this theory. Two articles by Sears (1942, 1948) likewise support the theory with evidence from vegetational changes and forest migrations since early Wisconsin time. Visher (1949), Devaney (1950), Kimble (1950), Larsen (1951), and McVaugh (1952), to mention a few others, also have presented supporting evidence. A large volume of literature based on bog pollen profile charts, or the pollen analysis method, also lends support to the theory.

In view of the fact that climax vegetation is considered to be "a single community, which is composed of the most mesophytic vegetation that the climate can support and whose moisture relations are average, or intermediate, for the region as a whole," (Oosting 1948, p. 224) it would appear that the relic status of the conifers in this deciduous community could be considered as further evidence in support of the theory of a warming climate for the area.

DIFFERENCES IN FOREST COMPOSITION IN RELATION TO SOIL SERIES

The 6 different soil series of this study are of the podzol group. The different profiles, characteristic of each series, compare favorably with the general descriptions of Wolfanger (1950, p. 38).

The quadrat data indicate that the Roselawn complex is the critical one when related to an expression of a climax northern hardwood community.

Dominance, as indicated by the DFD Index, indicates that such preclimax (Weaver & Clements 1938, p. 84) species as *Quercus rubra* var. *borealis* and *Q. alba* are important members of the community on Roselawn soil. The presence of *Acer saccharum, Fagus grandifolia, Ulmus americana* and *Tilia americana* is indicative of the extent that the course of succession has advanced towards the climax. *Pinus resinosa* is considered by Whitford (1901, p. 299) to indicate a transitory stage from the more xerophytic

Pinus banksiana to the less xerophytic *Pinus strobus*. Roselawn is the only one of the six soil series considered which contained *P. resinosa* within the quadrats.

The high dominance value attained by *Acer rubrum* on Roselawn soils might seem to invalidate the suggested xerarch subclimax status of the community. The species is common in late or subclimax stages of hydrarch succession and it is often a dominant on flood plains, where it frequently replaces *Acer saccharum* in poorly drained stands (Secor 1949, p. 76). However, *Acer rubrum* has a wide tolerance range and is almost as often found as a conspicuous member of invading deciduous forests on former pine plains. In a comprehensive study of the relation of soil characteristics to forest growth and composition in the Northern Hardwood Forests of Northern Michigan, Westveld (1933, p. 37) stated as one of his conclusions that: "Red maple and white pine are possibly more characteristic of the drier coarser textured soils than of the finer textured soils due to the lesser degree of competition of these sites which would react in favor of these relatively intolerant species." This factor, as defined by Westveld, is believed to account for the dominance of this species within the Roselawn community of this area.

The general description of the soil profile is indicative of the xeric nature of the soil series, yet there are some factors which would be favorable to invading mesophytic tree species. Probably the 8 in. of light yellow, loamy sand, forming the B_1 horizon, would especially favor the deciduous tree species characteristic of a mature (climax) northern hardwood forest.

There is some variation of relative dominance among secondary trees on the different soils. *Fagus grandifolia* is the dominant secondary species on both Emmet and Nester soils but its position is taken over by *Ulmus thomasi* on Arenac, Kalkaska, and Selkirk soils. This can be partially accounted for on the basis of the soil profiles for these two soil series and that the Kalkaska series is less acid and has better drainage. The Selkirk series is also less acid than the Emmet but drainage is imperfect in the Selkirk series. Arenac, likewise, is less acid than Emmet. It would appear that the lower acidity of these three soil series, as well as their coarser texture, in contrast to the Emmet and Nester complex, are factors which together offer better site conditions for *Ulmus thomasi*.

Difference in dominance of one species over another within a particular soil series may suggest a disclimax lociation. When such species as *Ulmus thomasi*, *U. americana* and *Acer rubrum* attain a higher degree of dominance than such species as *Fagus grandifolia*, *Tilia americana* and *Fraxinus americana*, the lociation may be considered to be further removed from the climax forest community than in instances where the latter species have attained greater dominance values. Thus, the lociation on Emmet soils (*Acer saccharum*, *Fagus grandifolia*, *Ulmus americana*, *Tilia americana*, *Fraxinus ameri-*

cana, *Ulmus thomasi*, *Prunus serotina* and *Ulmus rubra*) is more like the northern hardwood type of climax forest than the lociation on Arenac (*Acer saccharum*, *Ulmus thomasi*, *U. americana*, *Fagus grandifolia*, *Fraxinus americana*, *Tilia americana*, *Acer rubrum* and *Tsuga canadensis*).

FORESTS OF THE PAST AND THE PRESENT

At the time of the original land survey the forests of Missaukee County could be divided into four communities: swamp; pine; mixed conifer-northern hardwood; and hardwood (Fig. 8).

Four major changes have strongly affected the nature of the modern forests. First, there has been a great reduction in the amount of land now in forests when compared with that at the time of the original land survey. This is a natural result within a county which at the turn of the century was in the grip of the lumbering industry. A second major difference is the complete absence of the former pine communities. Here the ravages of lumbering and fire have taken their greatest toll. Much of the former pine land is now occupied by some phase of the Aspen association (Gates 1930) or is still similar in appearance to the vegetation as described by Livingston (1905, p. 28-29) for Roscommon and Crawford Counties (these two counties border Missaukee County on the east):

. . . over vast stretches originally covered with pine there are now no trees at all. There are some dwarfed *Quercus alba*, *Q. rubra*, *Acer rubrum* and a number of shrubs.

Among the lower forms occuring here may be mentioned *Rhus hirta*, *Monarda fistulosa*, *Pteris aquilina*, *Gaylussaca resinosa*, *Vaccinium canadensis*, *Comptonia peregrina*, *Solidago hispida*, *Hamamelis virginiana*, etc. The growth of sweet fern being so luxuriant that the numerous prostrate logs are often hidden from view.

It is very evident that the effects of former lumbering operations and subsequent fires has been enormous and that these disturbance factors have done much to retard the normal course of plant succession. The specific factors which are responsible for the long delay in recovery of vegetation of this area are yet mostly unstudied. The phytosociology of former pine lands and the autecology of the plants within the area offer a wide field for future studies.

Another noticeable change between the primary vegetation and its present appearance is the large reduction in the extent of swamp communities. Much of this reduction has come about as the result of modern tillage practices and the desire to reclaim more land for agriculture. Efforts of the State Conservation Department to improve wildlife habitats in the county have likewise resulted in changing the aspect of swamp communities.

Finally, the coniferous element of the mixed conifer-northern hardwood forest is much reduced. Other differences in the mixed conifer-northern hardwood and hardwood communities were more evident after analyzing the quantitative data of the area for both periods of time. At the time of the original

land survey, the former community was a Beech-Hemlock-Maple association. Now the community is predominately sugar maple, with beech, rock elm, American elm, basswood and white ash as the principle secondary elements. Hemlock and pine, while still present, are incidental. There has also been a shifting in dominance of the important secondary species within the hardwood community of "then and now." In the past this community was dominated by sugar maple with beech much more abundant. Today, *Acer saccharum* is even more predominant and the secondary species are more closely grouped in regard to their respective degree of dominance.

SUMMARY AND CONCLUSIONS

The phytosociology of the upland second growth hardwoods in Missaukee County is considered in relation to structural characteristics of the concrete community and synthetic characteristics of the abstract community. Quantitative data from 546 5 x 20 m quadrats, representing 98 stands on 6 different soil series, were analyzed and interpreted to establish the type of forest community now representative of the area.

On the basis of (1) the structural characters of the concrete community, as established by the quantitative quadrat studies, (2) the qualitative characters which are indicated by these analyses, and (3) the synthetic characters of the abstract community here considered, it would appear that the upland second growth hardwood stands of Missaukee County represent a disclimax. The disturbing agent is man who has here modified the vegetation chiefly through two cultural practices: pasturing in all of the woodlots (stands), and unselected cutting of trees for supplemental fuel supplies. The resulting disclimax has the dominant trees of the climax northern hardwood forest (*Acer saccharum, Fagus grandifolia, Tilia americana, Fraxinus americana, Betula lutea, Tsuga canadensis, Ulmus americana* and *U. thomasi* intermingled with such subclimax species as *Betula papyrifera, Quercus rubra* var. *borealis, Acer rubrum, Populus grandidentata, P. tremuloides,* and *Prunus pensylvanica.*

Further, it is apparent that various soil series support edaphic lociations within the community as a whole and that the composition of the forest now is quite different from the composition as interpreted from the original land survey.

The data support the contentions of Whitford (1901) and Quick (1923) that the whole lower peninsula of Michigan would support a Maple-Beech association given time for the vegetation to come into equilibrium with the climate. It would seem that the disturbance factors of pine lumbering and fires have essentially eliminated relic coniferous species as dominants in the area and that with reforestation the normal course of succession is toward a Maple-Beech association.

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REGIONAL ASPECTS OF THE LATE-GLACIAL AND POST-GLACIAL POLLEN SUCCESSION OF SOUTHEASTERN NORTH CAROLINA[1]

David G. Frey

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INTRODUCTION

The writer quite recently (1951) presented pollen diagrams for three cores from the sediments of Singletary Lake in the North Carolina Coastal Plain, one from each of the three sand basins underlying the more recent sediments. These diagrams, which extend well back into Wisconsin time, are substantially similar in their major features. They are the first published pollen diagrams for any of the very numerous "Carolina bays"[2] of the Atlantic Coastal Plain between Virginia and Florida. The question was raised immediately as to what extent the observed microfossil succession represented conditions peculiar to this one basin and its immediate surroundings, and to what extent it reflected regional changes in vegetation. To obtain information on this matter cores from seven other bays in the same general region were analyzed, and the results are presented here. As will be apparent, the succession in all the cores is the same in its gross aspects, and as a consequence it has been possible to construct a generalized pollen diagram for the region. Throughout this paper the term pollen diagram is used in its broad sense of including spores as well as pollen types.

[2] Physiographically a "bay" is an elliptical or obovate depression in the Atlantic Coastal Plain, oriented roughly in a northwest-southeast direction. Its dark organic sediments are usually sharply delimited from the surrounding sand. (See Prouty 1952, and Johnson 1942, for a discussion of the distribution and surface features of the bays.) Botanically the term "bay" refers to a particular type of swamp vegetation (Penfound 1952), which may or may not occur in a physiographic bay. In this paper the term bay is used in its physiographic sense. The vegetation now present in the physiographic bays varies greatly, depending mainly on frequency of fire and duration of hydroperiods (Wells 1928).

DESCRIPTION OF REGION

All the sites reported on in this paper are Carolina bays located in Bladen and Columbus counties in southeastern North Carolina (Fig. 1). The maximum airline dimension of the region concerned is approximately 40 mi.; but except for Lake Waccamaw all the sites are roughly in a line on the north side of and closely paralleling the Cape Fear River for about 20 mi.
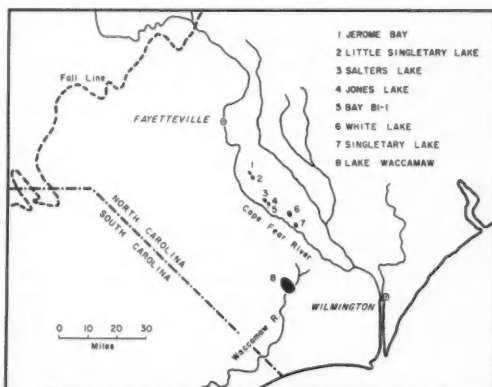
FIG. 1. General geographic location of the eight Carolina bays reported on in this paper.

In order to minimize as much as possible the effects of fire on the accumulated sediments and the effects of overrepresentation of the pollen of bog plants, most of the bays selected for study contain permanent bodies of water. These are: Lake Waccamaw, White Lake, Jones Lake, Salters Lake, and Little Singletary Lake, in addition to Singletary Lake

already reported on. Additional diagrams are presented for two filled-in bays without any persisting water surface at present: B1-1 just south of Jones Lake, and Jerome Bay, which Buell (1945, 1946a) has reported on incompletely. Buell very kindly made his hitherto unpublished data on Jerome Bay available for incorporation into this paper. Six of these bays vary in maximum length from 2000 to 4000 yd.; the maximum length of B1-1 is 930 yd. and of Waccamaw almost 11,000 yd. (Frey 1950). The morphometry of the present lake basins is summarized in a still earlier paper (Frey 1949).

METHODS

In each lake "soundings" to impenetrable sand or clay were taken with the $3/8$ in. steel rods of a Davis peat sampler every few hundred feet along a longitudinal transect, with further exploration where the sediments were deepest. The core of sediments was collected in each instance where the total penetrable depth was greatest. In the case of B1-1, the bay was entered on a compass course to its approximate center, with frequent soundings along the way, then additional soundings were taken for a hundred yards or so along each of several directions to determine that the point selected was in fact the deepest point that could be located with the expenditure of a reasonable amount of time and energy.

In Jones, Salters, and White lakes the superficial organic layer, which is often quite soft in consistency, was sampled with a Hiller sampler. All other samples were collected with a Davis peat borer. It was found by experiment that a new Davis sampler tends to fill by suction in soft limnic sediments, so that a stratified core is not obtained even though the opened sampler is pushed the required distance into undisturbed sediments. After sufficient wear, however, the piston fits loosely enough in the cylinder so that there is no tendency to fill by suction. All the samples in this series of cores are non-suction samples.

Samples were collected at 6-inch intervals from the surface of the sediments downward to the lower limit of penetration. The plugs were preserved in properly labelled vials and brought back to the laboratory for analysis. Unfortunately, it was not realized at the time of collection how rapidly the pollen composition in these basins could change over short vertical distances, particularly at the often sharp transition from the pine-spruce maximum to the overlying broadleaf maximum. Analysis showed that at least at some levels it would have been desirable to have samples for pollen analysis every inch or even every half-inch of depth. A number of the samples from these cores, however, were 3 or 4 in. long, permitting some intermediate levels to be analyzed. These instances will be readily apparent in the pollen diagrams to follow.

Organic samples were prepared by the standard technique of boiling in 10% KOH. Microfossils from predominantly inorganic sediments were concentrated by differential flotation in a bromoform-acetone mixture having a density of 2.3 g/cc (Frey 1951). The final concentrate was mounted in glycerine jelly containing gentian violet for differentiation. Counts were made by systematically moving a slide by means of a mechanical stage through the field of a microscope at a magnification of 440 diameters, and tabulating each pollen and spore as encountered. With two exceptions no count was terminated until at least 150 tree pollen grains had been identified. At those levels where Isoetes microspores were very abundant, an estimate of the number present was obtained by counting the microspores only in a 3 mm section of each row examined for tree pollens, and then adjusting the number counted by an appropriate factor based on the total length of the rows.

Pollen and spores were sufficiently abundant in the surface gyttja layers of the lakes so that the number of pollen grains per mm^2 of slide preparation could be regulated at will by the amount of sediment placed on the slide. Tree pollen densities of about 6 to 10 grains per mm^2 were found best, in that they permitted a count to be made quite rapidly and yet did not have too much material obscuring or masking the pollens and spores.

In the silt layers where the pollen is so greatly diluted by inorganic material that counts cannot be made on the unconcentrated material, tree pollen densities only slightly smaller than those for the organic sediments could be prepared in most instances by the bromoform method. For quite a number of samples from whitish silt, however, densities of only 0.3-0.6 grain per mm^2 could be prepared. Such slides necessarily took considerably longer time for examination.

In the construction of the pollen diagrams each bar is proportional to the number of that particular pollen or spore found, expressed as a percentage of the total tree pollens present at that depth. This is standard procedure in pollen diagrams of this type. All depths are referred to the surface of the sediments if these are at or above the water table, or to the top of the water in the lakes. In the latter instances the uppermost pollen spectrum in the diagrams represents conditions at or very close to the surface of the subaqueous sediments.

RESULTS OF INDIVIDUAL CORES

One always hopes that any particular core represents an uninterrupted interval of time with its associated vegetational changes. Where there are abrupt changes in the pollen curves, however, one suspects discontinuities in the sedimentation record. Disappointingly, there are quite a number of such abrupt changes in the diagrams to be presented, so that no single core, with the possible exception of Si-25, presents a complete pollen record.

Evidence is being presented in detail in another paper that the water surface areas of a number of these lakes have been recently expanding (Frey 1953). This expansion has resulted in an erosion of the littoral peat deposits, and a redistribution of these materials within the lake basin. Such phases of erosion

and redeposition have undoubtedly occurred at various other times in the ontogeny of these basins, with erosion obliterating parts of the record, at least peripherally, and redeposition confusing the record by admixture of pollen and spores from earlier sediments.

The record has also probably been affected by non-accumulation of sediments at various times. In some of the deeper horizons rootlets are occasionally found in growth position, indicating that the lake basins may have been experiencing various degrees of exposure at these times.

In spite of these deficiencies in the record, however, the major fluctuations in the pollen curves are the same from one diagram to another. This has permitted the generalized pollen diagram (Fig. 11) to be divided into a number of distinct pollen zones, designated for convenience by arbitrary symbols. To facilitate cross reference and discussion, the zones of the individual diagrams to follow will frequently be designated by the appropriate symbols.

Except for the upper deposits in Bay B1-1 and presumably in Jerome Bay as well, the sediments represented in this study are essentially limnic in origin. The layers which are primarily inorganic consist of fine silt and clay with usually no sand or only a small percentage. Sometimes, however, rather distinct sandy layers occur. The organic sediments usually contain only minor amounts of cellular plant

fragments, and these are mostly microscopic. Only in particular locations, such as Zone N (middle organic layer) at site Si-12, were macroscopic remains found. This layer promises to be richly rewarding to a botanist interested in identifying species of plants from seeds, fragments of leaves, etc.

SINGLETARY LAKE (Si-25)
(Figure 2)

Before considering the new pollen diagrams it is well to review the succession in Singletary Lake as a basis for comparison. Of the three diagrams published from this lake (Frey 1951), Si-25 is most significant and is here presented again in modified form. The essential features of this diagram are:

(1) Spruce pollen (Picea) appears at a certain level, and then continues in small percentages almost without interruption to the bottom of the core.

(2) A short distance below where spruce appears there is an extensive pine-spruce maximum (Zone M) with a minimum representation of broadleaf species. The upper part of this zone is considered contemporaneous with the Mankato maximum in late Wisconsin time (age 11,000 years in eastern Wisconsin, as listed by Flint & Deevey, 1951).

(3) Above the pine-spruce maximum there is a marked shift to a mesophytic broadleaf maximum of oak (Quercus), hickory (Carya), beech (Fagus), and birch (Betula), with some hemlock (Tsuga) also
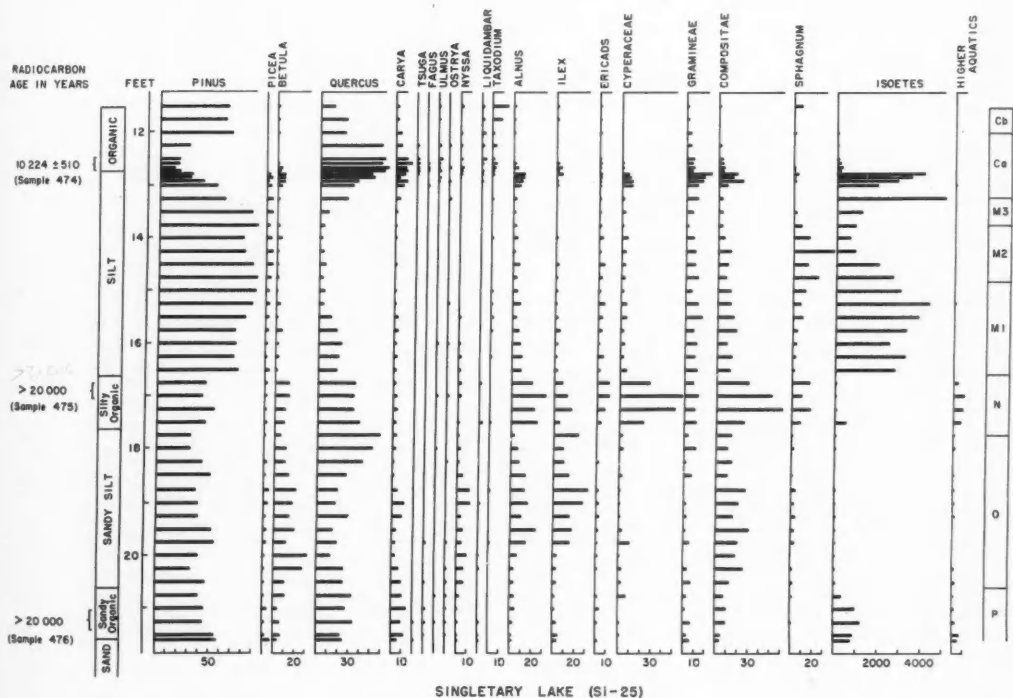
FIG. 2. Pollen diagram of core Si-25 from the southeast basin of Singletary Lake. (Modified from Fig. 1 in Frey, 1951.)

TABLE 1. Complete pollen and spore analysis of core J-1 from Jones Lake. All figures are percentages of the total tree pollens at each level.

Depth	Pinus	Picea	Quercus	Carya	Betula	Fagus	Tsuga	Castanea	Nyssa	Liquidambar	Taxodium	Acer	Ulmus	Fraxinus	Juglans	Salix	Ostrya	Carpinus	Platanus	Liriodendron	Total tree pollens	Alnus
6′ 7″	68.6		18.3	2.1		0.5		0.5	0.5	1.6	5.2	1.0	1.0						0.5		191	1.0
7′ 0″	65.5		23.0	1.8		0.4			1.8	1.3	4.0	0.4	0.9					0.4		0.4	226	0.9
7′ 6″	69.0		18.8	1.4						0.5	8.2	1.0	0.5					0.5			207	
8′ 0″	68.8		18.2	0.5						1.6	7.3	1.6	1.0						0.5		193	
8′ 6″	62.9		17.0	1.3		0.6		0.6		3.8	6.9	2.5	1.3	0.6			1.3	0.6			159	0.6
9′ 0″	65.9		12.3	1.7	1.1	0.6			2.2	0.6	11.7	2.2	0.6	0.6					0.6		179	1.1
9′ 6″	67.1	0.3	22.5	2.4		1.8			0.6	1.2	1.8	1.2	0.6			0.6					169	1.2
10′ 0″	89.2	3.2	5.7		1.3							0.6									158	1.3
10′ 6″	88.1	5.4	5.4										0.5				0.5				186	1.1
11′ 0″	92.2	3.1	4.1										0.5								194	0.5
11′ 6″	95.4	3.0										1.1					0.5				185	2.2
12′ 0″	96.3	3.0	0.7																		153	0.7
12′ 6″	91.9	7.5	0.6																		161	1.9
13′ 0″	92.4	7.0	0.6																		158	
13′ 6″	95.6	1.5	1.2	0.6	0.6								0.6								173	1.7
14′ 0″	90.1	3.1	4.9	0.6	0.6													0.6			163	2.5
14′ 6″	89.3	1.5	9.2																		163	1.8
15′ 0″	88.1	0.3	8.5											1.2	0.6	1.2					165	2.4
15′ 6″	86.5	1.6	7.0	1.3	1.3				0.6	0.6		0.6	0.6								158	3.2
16′ 0″	71.5	0.6	20.0	2.4	3.0	0.6			0.6							0.6	0.6				165	6.1
16′ 4″	46.5	2.3	26.7	4.7	3.5			4.7	3.5				2.3			2.3	1.2	1.2		1.2	86	16.3
16′ 6″	59.6	3.1	21.4	3.7	1.8				2.4		0.6	1.8	1.2			1.8	2.4				164	12.2
17′ 0″	89.8	4.2	2.4	1.8	0.6							0.6					0.6				169	1.2
17′ 6″	89.2	1.2	5.4	1.8	1.8			0.6									0.6				168	4.2
17′ 8″	49.4	1.3	28.5	8.2	5.1		0.6		2.5	1.3		0.6	1.3				0.6	0.6			158	3.2

occurring (Zone *Ca*). The radiocarbon age of the central portion of this maximum is $10,224 \pm 510$ years (sample 474 in Libby 1951).

(4) The changes in and above the broadleaf maximum suggest the *C1*, *C2*, and *C3* zones established by Deevey (1949) for the northeastern glaciated area, culminating in the present pine subclimax of the southern Atlantic Coastal Plain.

(5) Below the pine-spruce maximum there is a second organic layer (Zone *N*), characterized by an abundance of non-tree pollens, such as Alnus, Ilex, grasses, composites, and sedges, and a well marked maximum of higher aquatics. The radiocarbon age of this layer is greater than 20,000 years (sample 475 in Arnold & Libby 1951).

(6) At a still greater depth there is a third and less pronounced organic layer (Zone *P*), likewise (naturally) with a radiocarbon age greater than 20,000 years (sample 476 in Arnold & Libby 1951).

(7) Between the middle and upper organic layers there is a tremendous abundance of Isoetes microspores, amounting to more than 5000% at one level. (These figures for Singletary Lake are actual counts rather than estimates). Isoetes recurs, although in lesser abundance, in Zone *P*.

(8) Below the second organic layer occur rather complicated fluctuations of the broadleaf trees and some of the non-tree species (Zone *O*). This stratum is predominantly inorganic.

The other cores described in the 1951 paper have the same general succession, except that the pollen records do not extend back so far in time. Core Si-22 from the filled-in northwest section of the bay demonstrates that most of this filling process has occurred since the broadleaf maximum.

A reexamination of the material in core Si-25 has demonstrated on the basis of greater experience in working with pollens that the grains reported as Carpinus in the 1951 paper are more likely Ostrya, even though these two genera are very difficult to separate. The percentage occurrence of Ostrya is shown in Fig. 2.

JONES LAKE (J-1)
(Figure 3; Table 1)

The pine-spruce maximum (Zone *M*) is well developed, as in Si-25, although the shift to a broadleaf maximum and subsequent readjustment to a pine predominance is obscured. Presumably these extensive changes occurred in the 6-in. stratum between 9.5 and 10.0 ft. below the surface. The plug of sediments from the 9.5 ft.-level was too short to permit examination of additional horizons at slightly greater depths to determine whether the shift actually is compressed into a vertical distance of less than 6 in., or whether it is largely missing from the record.

Although no distinct second organic layer is present, the silt becomes darker toward the bottom of

Ilex	Ericads	Corylus	Myrica	Gramineae	Composites	Artemisia	Ambrosia	Cyperaceae	Chenopods	Caryophyllaceae	Nuphar	Nymphaea	Myriophyllum	Isoetes microspores	Lycopods	Polypods	Asplenium	Osmunda	Sphagnum	Dinoflagellates	Unidentified	Depth
1.0	2.1			2.1	2.1										0.5				0.5		16.8	6' 7"
1.3	0.9			0.4											0.4				1.3		16.4	7' 0"
		1.4		0.5									1.0		0.5					0.5	10.1	7' 6"
			0.5	1.6										0.5		0.5					21.3	8' 0"
				1.3									1.9	1.9						5.0	27.7	8' 6"
	0.6			0.6				0.6			0.6	0.6	0.6	0.6		0.6			0.6	8.4	25.7	9' 0"
				6.5	1.2			0.6	0.6					17.2						0.6	95.0	9' 6"
	0.6			5.1	0.6			1.3						368	1.3				0.6	6.3	44.4	10' 0"
				2.7	2.7			3.8	0.6			0.5	0.5	797	0.5				1.6	2.2	16.1	10' 6"
				7.2	2.1			5.7						729		0.5			1.5	6.7	11.8	11' 0"
	0.6			1.6	1.1			1.1						902			0.5		0.5	1.6	10.8	11' 6"
				0.7				2.6						387	2.0				2.0	1.3	12.4	12' 0"
		0.6		3.1	1.2			5.6						345	10.6	1.2			6.9	9.3	26.8	12' 6"
	0.6			1.9	1.3			1.9						1360	1.9				3.2	6.3	17.1	13' 0"
	0.6	0.6		5.8	7.5			2.9						1010	1.2			0.6	3.5	6.4	16.8	13' 6"
	4.3	1.2		11.7	11.0	0.6		9.2		0.6				3760	1.2	0.6			6.1	3.1	36.2	14' 0"
	0.6	0.6		7.4	4.3			2.5						4760	1.2				3.7	3.7	34.4	14' 6"
	3.6	1.2		17.6	12.8			6.7		0.6				4470	2.4				2.4	4.9	49.8	15' 0"
2.5	5.1			10.1	4.4			5.7					0.6	5320	0.6	0.6	0.6		6.3	1.3	66.4	15' 6"
0.6	6.7		0.6	12.1	14.5			10.3						1630	3.0	1.2			8.5	8.5	76.4	16' 0"
5.8	9.3	2.3		39.5	39.5			10.5	1.2				1.2	1.2	1340	1.2	2.3	2.3	16.3	5.8	327	16' 4"
4.9	8.6	0.6		33.6	17.1			7.9		1.2				3230	0.6	1.8	0.6		2.4	23.8	133	16' 6"
	4.7			3.0	3.6			4.7						199	2.4	1.8	3.6		7.7	3.6	29.7	17' 0"
	1.8	0.6		10.7	4.8			3.6					0.6	1480	0.6		1.2		4.2	0.6	45.2	17' 6"
5.1	3.2	0.6		30.4	7.0		0.6	3.8			0.6		1.3	3790					0.6	8.9	134	17' 8"
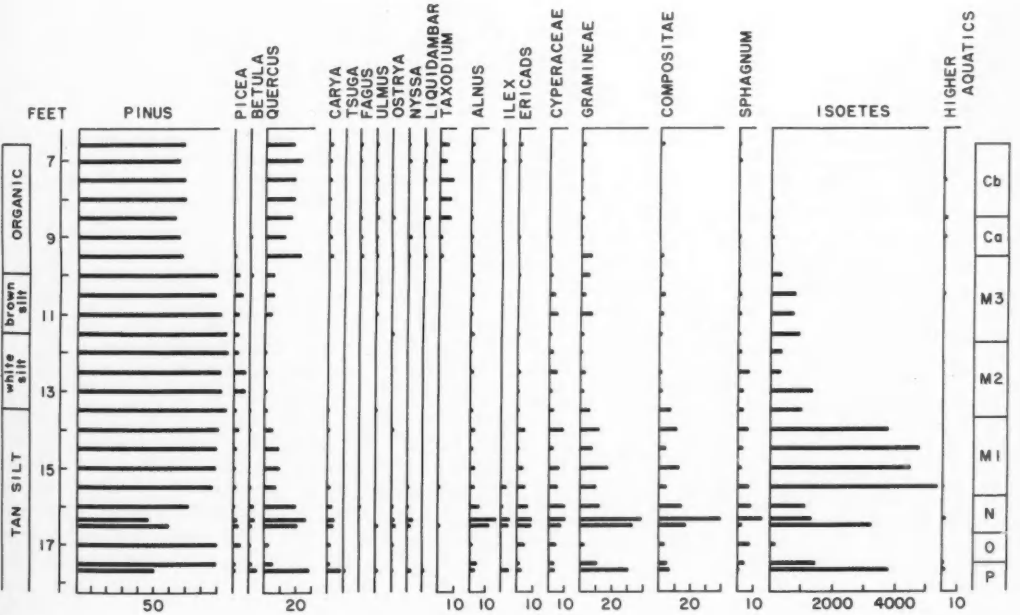
JONES LAKE (J-I)

FIG. 3. Pollen diagram of core J-1 from Jones Lake.

TABLE 2. Complete pollen and spore analysis of core Bl-1 from a small bay near Jones Lake. All figures are percentages of the total tree pollens at each level.

Depth	Pinus	Picea	Abies	Quercus	Carya	Betula	Fagus	Tsuga	Castanea	Nyssa	Liquidambar	Taxodium	Acer	Ulmus	Tilia	Fraxinus	Juglans	Salix	Ostrya	Magnolia	Gordonia	Liriodendron	Populus
1' 0"	49.2			13.9	0.7	0.7			1.3	27.1	4.0	1.3		0.7								0.7	0.7
1' 6"	36.4			17.3	0.5	0.5			0.5	30.5	1.5	2.0								1.0	9.7		
2' 0"	31.4			10.3	1.7	0.6				41.7	2.9		1.1	0.6		0.6				6.9	1.1	1.1	
2' 3"	27.6			13.8	2.2	0.6				50.8	1.1	0.6	1.7			0.6				0.6	0.6		
2' 6"	41.0			8.0	1.1					43.1	0.5	1.6	1.1							3.2	0.5		
2' 8"	60.2			5.3	1.2				0.6	26.9	3.5		0.6						0.6	0.6	0.6		
2'10"	45.8			15.9	1.9	1.3				25.5	1.3	1.3	3.2	1.3					0.6	0.6			1.3
3' 0"	27.1			9.4	1.0					54.6	2.5	1.0	1.0		1.0			0.5		2.0			
3' 6"	28.1			11.4						56.3	0.6		1.2	0.6						1.8			
4' 0"	16.1			15.0		0.6	0.6			65.5	0.6		0.6						0.6	0.6			
4' 6"	16.1			19.1		0.6	1.8	+		51.2	4.8	2.4	0.6	1.2						1.2	1.2		
5' 0"	12.4	0.6		14.7		2.4	4.7			59.4	1.8	1.8		0.6						0.6	1.2		
5' 6"	7.0	0.6		43.9	18.5	3.8	4.5		0.6	8.9	2.5			0.6			0.6			6.4	0.6		0.6
6' 0"	19.3	2.5	0.3	39.2	21.8		3.7	0.6		1.2	0.6	0.6	0.6	1.2						6.8	0.6		0.6
6' 3"	18.1	3.6		43.3	15.3	1.6	4.4	0.5		0.5	0.5			1.6		1.1				9.3			
6' 6"	30.2	1.7	0.9	30.7	26.2	0.6	2.8	0.6		0.6				0.6						4.6			0.6
6' 8"	28.7	2.9	+	36.3	20.5	1.2	4.1				0.6			0.6						5.3			
6' 9"	20.1	2.8		35.1	26.6	1.7	5.1									2.3				6.2			
6'10"	19.1	2.2		37.7	18.6	1.1	6.6				0.5		2.2	2.7		0.5				8.2			0.5
7' 0"	42.5	2.8	1.2	20.3	25.2	0.6	1.8						0.6	1.8					3.1				
7' 2"	67.2	2.6		23.6	4.6		0.7							0.7					0.7				
7' 4"	83.8	9.0		5.8		0.6										0.6							
7' 6"	85.7	9.0		3.9																			1.3
7' 8"	91.6	7.0		1.3																			
8' 0"	89.1	5.5		4.3		0.6													0.6				
8' 2"	93.0	2.3		3.3									0.7						0.7				
8' 4"	95.0	3.1		1.9																			

the core, and the characteristic abundance of non-tree species associated with this organic layer in Singletary Lake occurs, especially at 16.3 and 16.5 ft., indicating that this level is equivalent to Zone N at site Si-25. The recurrence of beech, hemlock, tupelo (Nyssa), and sweetgum (Liquidambar) substantiates this conclusion.

The trends in fluctuation of sedges, grasses, and composites in and below this non-tree maximum correspond to those found in Zone O of Si-22 (Frey 1951), and the abundance of Isoetes microspores at the extreme bottom of the core suggests the third organic layer (Zone P) of core Si-25. At any rate the time interval represented in the lowest 2 ft. of this core is very compressed, and the sediments are probably incapable of satisfactory analysis except on the basis of samples collected at much closer intervals.

The abundance of Isoetes microspores in this core surpassed even that in core Si-25: at 15.5 ft. this spore amounted to 5320% in terms of total tree pollens at the same level.

BAY B1-1
(Figures 4 & 5; Table 2)

B1-1 is a small bay approximately 930 yd. long, located less than ½ mi. southwest of Jones Lake. The bay is completely filled in with organic sediments, on the level surface of which there is a dense tangle of trees and shrubs, many of them broadleaf evergreens. When sampled on August 5, 1949, the bay was dry, with only scattered patches of Sphagnum in moist places, indicating at least the temporary occurrence of hydroperiods.

The bottom of this core appears to be at or near the pine-spruce maximum. In the silt overlying the sand there is a gradual shift to a well-developed broadleaf maximum. The progressive nature of this shift indicates that the bay was actively accumulating sediments during this time interval, unlike some of the other bays investigated where there was little or no transition, as, for example, the pollen diagram for core Si-22 (Frey 1951) or the preceding diagram for Jones Lake (Fig. 3).

The broadleaf maximum is characterized by peaks of oak and hickory, and, in this case, a less pronounced peak of birch, as well as a minor occurrence of hemlock. Isoetes and spruce disappear near the upper part of this Ca zone.

In Zone Cb above the broadleaf maximum there is a striking dominance of tupelo, which continues almost to the surface. The lack of abundance of cypress (Taxodium), in contrast to core Si-22 from the filled-in northwest end of Singletary Lake, may well indicate that after the broadleaf maximum the bay was not nearly continuously under water, but rather was more seasonally flooded. (See Oosting 1948, for a discussion of the relation between dura-

Total tree pollens	Alnus	Ilex	Ericads	Corylus	Myrica	Gramineae	Compositae	Artemisia	Cyperaceae	Chenopods	Caryophyllaceae	Nuphar	Nymphaea	Myriophyllum	Sagittaria	Isoetes microspores	Lycopods	Polypods	Asplenium	Sphagnum	Dinoflagellates	Unidentified	Depth
152	0.7	2.0	1.3	....	1.3	0.7	1.3							0.7							23.1		62.6	1' 0"
197			1.0	....	0.5	0.5	0.5												1.0		31.0		51.9	1' 6"
175	0.6	2.3	0.6	....			1.7												1.1		6.9		42.3	2' 0"
181			2.2	....															0.6		13.8		27.1	2' 3"
188		1.6	0.5	....	1.1														0.5		19.2		33.5	2' 6"
171					0.6		0.6							0.6							12.9		55.0	2' 8"
157	1.3	0.6	2.5	....	0.6		1.3												1.9		21.7		84.6	2'10"
203	1.0	2.0	0.5			1.0	0.5												0.5		4.9		48.3	3' 0"
167		0.6	0.6				1.2												0.6		6.0		53.9	3' 6"
180			1.1																0.6		7.2		71.1	4' 0"
168	1.2	3.6	0.6	1.2		0.6	0.6		0.6			0.6							1.8		9.5		87.5	4' 6"
170		4.1	1.8			1.8	2.4					0.6	1.2						0.6		5.3		67.6	5' 0"
157	1.9	0.6	0.6	1.3		0.6	1.3		1.9	0.6		1.3	7.0			57.3	0.6			0.6		75.1	5' 6"
161	1.2	1.9				0.6	3.1		0.6					0.6		123				0.6	9.3	61.7	6' 0"
183	3.3	3.3	0.5	0.5		4.9	2.2		0.5			1.1	2.7	1.1		178	1.1	0.5		0.5	7.7	71.7	6' 3"
176		1.7				3.4	1.1		1.1			1.7	1.7			66.6	2.8		1.1	11.4		49.0	6' 6"
171	0.6	2.3		1.2		3.5	1.8			0.6		1.2				113				10.5		63.1	6' 8"
176	2.3			0.6		2.3	1.1			0.6		0.6	1.7		0.6	167	1.7	0.6		0.6	6.8	62.3	6' 9"
183	2.7	1.6		3.3		1.1	0.5	0.5					0.5		0.5	111	1.1				4.9	38.8	6'10"
163	1.2	1.2	0.6	1.2		1.8			0.6		0.6	0.6				50.5	0.6	0.6		2.5	4.3	25.2	7' 0"
153	0.7		2.6			2.0	2.6									41.9		0.7	0.7	1.3	7.2	22.9	7' 2"
155	1.3		1.9	2.6	1.3	1.9	1.9	1.3								72.9	3.9		1.9	5.8	1.3	33.5	7' 4"
155	0.6		1.3	2.6	1.3	0.6	3.9	0.6							0.6	70.3			0.6	7.1	3.9	23.9	7' 6"
156	1.3		0.6	1.3	1.3		2.6	1.3				0.6	0.6			45.5				3.8	0.6	21.8	7' 8"
165	1.2		0.6	0.6		1.2	3.0	2.4			0.6		1.2		0.6	27.9	0.6	0.6	0.6	1.8	0.6	27.3	8' 0"
152	2.6		0.7			2.0	4.6	2.0	3.3	0.7					0.7	32.3	2.6			6.6	1.3	33.7	8' 2"
161	1.2	0.6	2.5	1.2	1.2	3.1	3.7			0.6						40.4	1.2		1.2	2.5	0.6	33.5	8' 4"

tion of hydroperiods and vegetation.) This interpretation is substantiated by the occurrence of sponge spicules, which are abundant from the 7.5 ft.-level to the top of the broadleaf maximum at 5.5 ft., but then disappear almost entirely. The two peaks of Sphagnum which seem to alternate with two peaks of tupelo occur also in core Si-22, and seem to suggest two drier periods with surface water confined to isolated shallow puddles as at present.

In pollen diagrams from the glaciated region the percentage representation of all tree genera is commonly shown. This has not been done with the Coastal Plain diagrams thus far, because quite a number of the tree pollens are sporadic in occurrence and do not appear to have any particular indicator value. The present core (B1-1) has perhaps the best diversity of arboreal species found in cores analyzed to date, and for that reason a diagram is presented showing all arboreal genera identified. It is apparent in Fig. 5 that quite a number of the 23 genera of trees shown occur so erratically and in such small numbers that little significance can be attached to their presence. However, an additional fact is apparent from this diagram: the late appearance of such genera as Magnolia, Liriodendron, and Gordonia may well mean that these distinctly southeastern types did not move into (or back into) the North Carolina Coastal Plain until quite recently. This matter will be taken up again in the discussion.

It should be noted that core B1-1 was the last one of this series studied, and the first one in which Magnolia and Gordonia were definitely identified and tabulated. Reexamination of the other cores has shown, however, that these trees occur at corresponding levels in them, but no attempt was made to recount the samples.

SALTERS LAKE (Sa-1)
(Figure 6; Table 3)

As was found in the sediments of nearby Jones Lake, the sediments of Salters Lake exhibit a well-developed and prolonged pine-spruce period (Zone M), but almost nothing that might be called a broadleaf maximum. At the 10.75 ft.-level small percentages of hemlock, tupelo, and sweetgum appear, after having been completely lacking from the preceding strata. However, there is little suggestion of the extensive development found in Si-25 and B1-1. Either conditions within the basin at this time were not favorable for accumulation of sediments, or else the sediments dating from this time were later destroyed at this site by subsequent reworking of the materials by currents and organisms. Additional cores from other places in the basin are needed to decide the point.

Midway through the pine-spruce period there is a slight but distinct increase in oak and hickory, with concurrent or semi-concurrent increases in
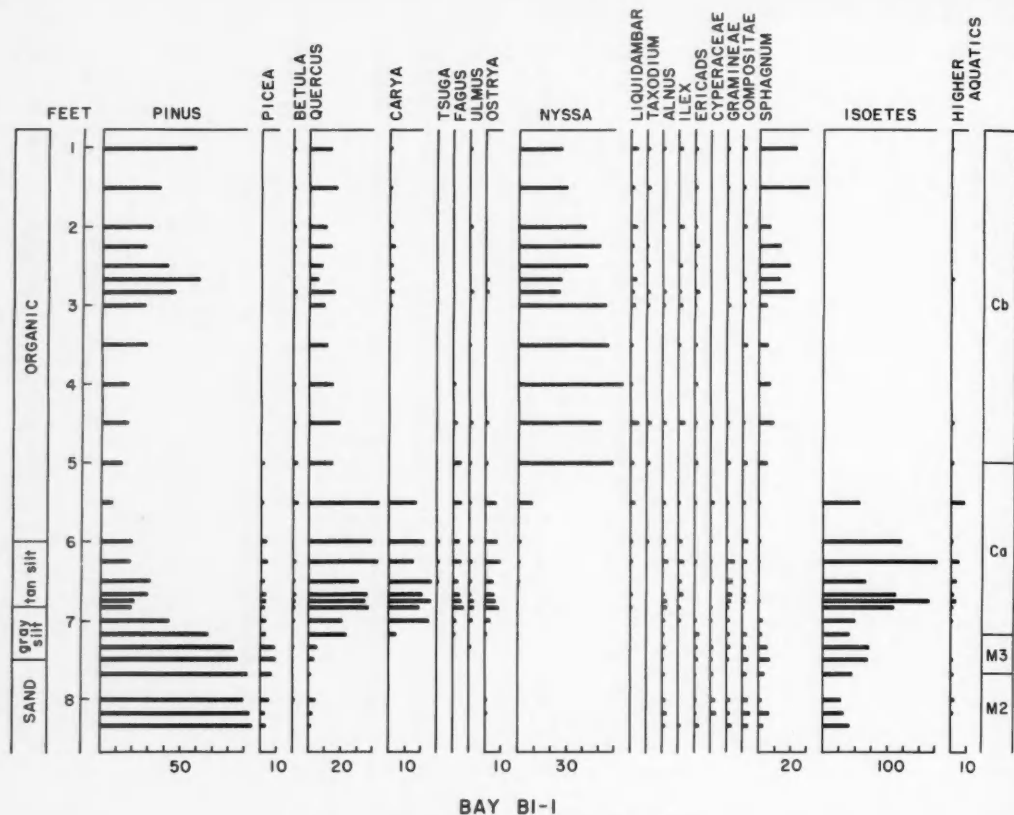
FIG. 4. Pollen diagram of core from Bay Bl-1.

heaths, sedges, and grasses (Zone *M1*). The pollen diagram for Si-25 (Fig. 2) suggests a somewhat similar shift in pollen composition.

A second organic layer is prominent in the diagram, and it exhibits the high percentages of non-tree species which appear to be regionally characteristic of this stratum. Although percentages of non-arboreal pollen (NAP, in customary designation) are high throughout this interval in Salters Lake, the layer might well be divided into the *N* and *O* zones. The basis for this division is the large representation of Sphagnum in the upper half, the apparent peak of oak midway through with a distinct minimum near the bottom, and the general low abundance of Isoetes. Evidence for the contrary view is the fact that likewise in cores Si-12 and Si-22 there is a peak of Sphagnum near the top of this layer and a peak of higher aquatics near the bottom. The irregular nature of the pollen curves within this second organic layer suggests there may have been a certain amount of reworking of the sediments.

WHITE LAKE (Wh-1)
(Figure 7)

Sediments deeper than 3.5 ft. could not be found in White Lake. These include a silty organic layer

1 ft. thick, overlying a white or bluish clay. The bottom portion of the clay is indurated and consolidated with iron, so that samples were obtained only with great difficulty. Rootlets in a vertical position in the clay indicate that the lake was probably dry or nearly so during certain more recent periods. Pollen was so scarce below 11.5 ft. that even with the differential flotation technique counts could not be made.

In the 2.25 ft. of pollen-containing sediments there is relatively little differentiation, which is undoubtedly a reflection of frequent reworking of the sediments by currents. Spruce first occurs at 10.25 ft., and is present from that level to the bottom. This foot of sediments may therefore correspond to the pine-spruce maximum of the other cores, except that the broadleaf species, including hemlock and beech, are present.

Above a depth of 10 ft. there is an increase in oak, and a greater representation of other broadleaf genera, indicating that this foot of sediments probably represents post-glacial time. This is supported in part by the Isoetes curve, no spores of this pterido-phyte being present above 10 ft. In fact on the basis of the typical relationship of the Isoetes curve
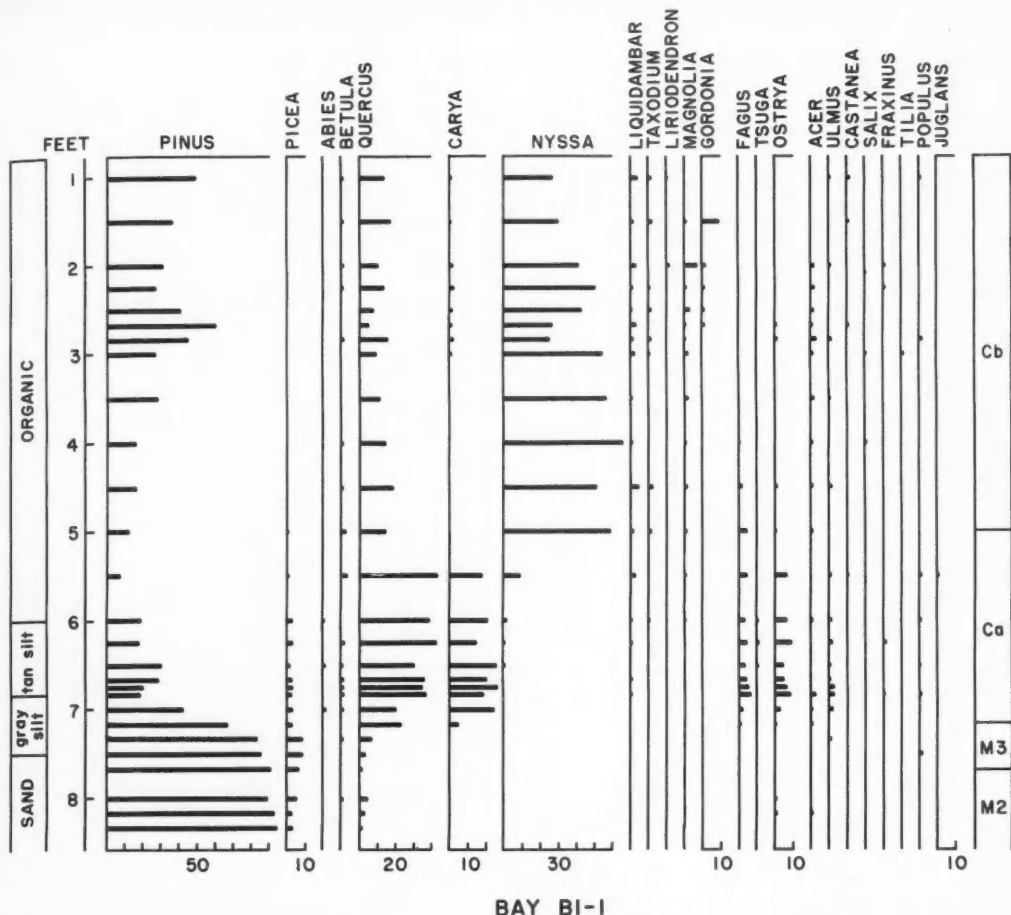
FIG. 5. Pollen diagram of core from Bay Bl-1, showing the percentage occurrence of all tree genera identified.

BAY BI-I

and of the spruce curve to the broadleaf maximum, and also on the basis of the occurrence of hemlock and beech in the present diagram, one is inclined to regard everything down to 10.5 or even 11 ft. as being post-glacial. The latter opinion is represented by the designation of zones in the pollen diagram.

It seems clear that pine is greatly over-represented in this diagram in relation to other arboreal types, even more so than it usually is. The reasons for this are not known.

LAKE WACCAMAW (Wa-1)
(Figure 8)

The sediments of Lake Waccamaw resemble those of White Lake in the occurrence of bluish clay at the bottom of the section and in the almost complete lack of pollen from this material. The ⅜-in. rod of the Davis peat sampler could be pushed down to a total depth of 16 ft., as measured from the surface of the lake, but the lowermost sediments were so compacted that the sampler itself could be worked down only to 14.7 ft. with great effort.

The pollen diagram from Waccamaw, however, is better developed and more easily interpreted than is the one from White Lake. The two lowermost spectra are from the upper part of the pine-spruce maximum (*M3*). In the 1-in. interval between 12 ft. 7 in. and 12 ft. 6 in. there is a radical shift to a broadleaf maximum, which in its development as here illustrated shows a good representation of oak, hickory, beech, elm (Ulmus), hophornbeam (Ostrya), and lesser percentages of hemlock, birch, tupelo, and sweetgum. Such a radical shift in composition in just one inch of sediments, as in other similar instances (J-1 and Sa-1), suggests a discontinuity in the sedimentation record.

Toward the top of the section is the typical increase in pine and a non-typical decline in oak to a very low percentage. The latter is accounted for in part by the very extensive occurrence of a pollen grain which has been called Chamaecyparis (swamp white-cedar), and this in turn is replaced at the surface by cypress. The grains assigned to Chamaecyparis had the same general appearance as those of Tax-

TABLE 3. Complete pollen and spore analysis of core Sa-1 from Salters Lake. All figures are percentages of the total tree pollens at each level.

Depth	Pinus	Picea	Abies	Quercus	Carya	Betula	Fagus	Tsuga	Castanea	Nyssa	Liquidambar	Taxodium	Acer	Ulmus	Tilia	Fraxinus	Juglans	Salix	Ostrya	Carpinus	Platanus	Total tree pollens	Alnus
9' 1"	69.3			16.7	0.5	0.5				7.3	1.0	2.6	0.5	1.0				0.5				192	0.5
9' 6"	61.5			15.4		1.8				12.4	1.8	5.9	0.6			0.6						169	0.6
10' 0"	62.3			19.7	1.6	0.5				8.7	1.1	6.0										183	0.5
10' 6"	60.3			22.7	3.1	0.5			0.5	5.7	0.5	4.1	1.0	1.0				0.5				194	1.5
10' 9"	83.0	5.1		7.8	1.8		0.6			0.6	1.2											168	
11' 0"	82.6	7.0		5.2	3.5														1.7			58	8.7
11' 6"	93.0	5.2		1.2	0.6																	172	
12' 0"	97.0	1.8		0.6		0.6																167	1.2
12' 6"	96.3	2.5		1.1																		178	0.6
13' 0"	85.1	1.0		7.6	1.9	0.6				2.5			0.6						0.6			158	10.2
13' 6"	81.3	2.1		11.0	4.3	0.6											0.6					164	5.5
14' 0"	89.7	1.1		5.1	1.7	0.6								1.1			0.6					175	1.7
14' 6"	91.5	2.5	0.5	3.8					0.5					0.5					0.5			183	1.1
15' 0"	95.3	1.8		1.8	0.6					0.6												170	1.2
15' 4"	66.2	1.7	0.3	22.5	1.3	2.0				3.3	0.7		0.7			0.7			0.7			151	35.1
15' 5"	40.2	0.9		44.0	4.3	3.7			0.6	1.9			1.2	2.5		0.6						162	50.7
15' 6"	35.5	1.9		42.8	6.4	7.7			0.6	2.6			1.3					0.6	0.6			157	72.8
15' 7"	31.9	1.3		40.4	4.4	12.6	0.6		1.3	2.5			3.2	1.3					0.6			159	66.2
15' 8"	38.5	+		21.1	1.2	34.8	+		0.6				1.9	1.2		0.6						161	212
16' 3"	36.3	2.5		24.2	0.6	27.4	1.9		1.3	1.9		0.6						0.6	2.5			157	167
16' 4"	31.4			23.1	1.9	35.3			4.5	1.9		0.6	0.6		0.6							156	192
16' 5"	47.9	0.6		23.8	1.3	20.1			1.3			0.6	1.9				0.6		0.6		0.6	160	218
16' 6"	35.9	0.7		23.5	2.6	31.4				2.6		2.6	0.7									153	290
16' 7"	28.1			54.4	0.6	9.7	+		1.3	3.2			0.6	0.6					0.6		0.6	155	65.3
17' 0"	20.4			48.6	2.6	16.2	2.6		0.6	2.6		0.6	2.6	1.3				1.3			0.6	155	129
17' 1"	21.5			44.9	4.4	20.9	1.9		0.6	1.3		0.6	1.9			0.6			1.3			158	137
17' 2"	20.3			50.8	1.3	15.4	3.2			3.2		0.6	2.6						2.6			156	123
17' 6"	16.3			51.2	2.6	16.6	1.9			3.8		0.6	3.8					0.6	1.9	0.6		157	135
18' 0"	68.7			12.8	3.8	10.2	0.6			1.9			1.3					0.6	0.6			157	21.7
18' 1"	64.5	1.3		17.4	5.2	9.0				1.3			0.6						0.6			155	32.9
18' 2"	44.1	+		27.3	1.2	14.9	1.2		1.2	2.5	+	0.6	3.1					2.5	1.2			161	80.7
18' 3"	32.7	0.6		33.7	3.2	18.4			1.3	1.3	0.6		4.4	0.6					3.2			158	165

odium, except that they lacked a papilla and had a considerably thinner, more irregular exine.

One of the striking ways in which this pollen diagram differs from all the others reported thus far is in the negligible occurrence of Isoetes microspores. Lake Waccamaw at the present time has water which is slightly alkaline, whereas all the other lakes have strongly acid water (Frey 1949). If the same chemical conditions prevailed in late glacial time, this alkalinity (including a greater calcium content) may have been a deciding factor in curtailing the abundance of Isoetes, which tends to thrive in oligotrophic situations. Radford (1950) observed that the present species of Isoetes occurring in North Carolina are never found in or near the highly acid "black water" streams and ponds of the coastal plain or mountains. If the species represented in the pollen diagrams (and *I. englemanni* may be one of them; see the section "Size-frequencies of Isoetes microspores") had similar preferences, then conditions in and surrounding the Bladen County lakes must have differed considerably during the *M* and *P-Q* periods from those of the present. Furthermore, the gradual disappear-

ance of Isoetes during *Ca* time may be associated with the gradual increase in littoral peat deposits and associated increasing color of the water.

JEROME BAY

(Figure 9)

Jerome Bay has the distinction of being the first of these peculiar oval depressions in the southern Atlantic Coastal Plain to have anything concerning its sediments and the microfossils contained in them. In two notes appearing almost simultaneously Buell (1945, 1946a) commented briefly on pollen occurring in the lowermost horizons in this bay. One type of pollen amounting to 12% of the tree pollens at a depth of 8.5 ft. was incorrectly listed as Abies. At Buell's request this listing is herein corrected to read Picea. On the basis of the occurrence of spruce pollen and of a small pine pollen claimed to be *Pinus banksiana* by virtue of its size-frequency characteristics, Buell concluded that these lowermost sediments dated from Wisconsin time. Buell never published a pollen diagram for Jerome Bay, wishing to check his results before doing

Ilex	Ericads	Corylus	Myrica	Cornus	Rhamnus	Gramineae	Compositae	Cyperaceae	Chenopods	Polygonum	Nuphar	Nymphaea	Myriophyllum	Sagittaria	Isoetes microspores	Lycopods	Polypods	Asplenium	Osmunda	Sphagnum	Dinoflagellates	Unidentified	Depth
1.0	1.0		1.0			2.1	1.0													1.6	0.5	25.0	9' 1"
0.6	0.6		1.8			1.8										0.6				2.4		27.2	9' 6"
0.5	2.7		2.2			1.1									0.5	0.6				2.7		38.3	10' 0"
1.5			1.0			2.1									1.5					1.0	1.5	21.7	10' 6"
	0.6					3.6	2.4	1.8							315					3.0	13.7	37.6	10' 9"
3.5	7.0	1.7				15.6	8.7								243	5.2	7.0			1.7		113	11' 0"
						2.3	1.2	1.7							40.7							2.9	11' 6"
0.6						0.6	2.4	3.6							357	0.6				1.8	1.2	4.2	12' 0"
	0.6					2.3	1.7	2.8							289	1.7	1.1	0.6		2.3	3.4	10.1	12' 6"
1.3	4.4	0.6				27.3	4.4	7.0							596	2.5	3.2	0.6		5.7	68.5	105	13' 0"
	2.4	0.6				7.3	4.9	5.5		1.2					93.5	1.8			2.4	2.4	25.1	39.1	13' 6"
		0.6				8.0	0.6	2.9							22.9	10.9	5.1	3.4		4.6	13.1	45.7	14' 0"
0.5						1.6	0.5	3.3				0.5	0.5		98.9	2.7		3.3		3.3	4.9	22.4	14' 6"
						1.8		1.8							49.4	1.2		1.8		0.6	11.2	13.5	15' 0"
0.7	9.9					10.6	19.2	41.7			2.0	1.3	1.3		207	4.0	6.0	1.3		37.1	6.0	192	15' 4"
1.9	14.9	1.2				8.7	21.1	35.3			1.2		1.9		364	3.1	5.6			49.5	0.6	354	15' 5"
3.8	17.9	0.6				8.9	17.9	46.0				1.3	0.6		57.1	2.6	3.2			69.6	0.6	336	15' 6"
1.9	16.4	1.9				11.4	23.3	79.5	0.6		0.6		1.9		8.8	1.9	5.0	1.3		43.5		322	15' 7"
9.9	9.9	2.5				9.9	22.4	35.4	0.6				1.2		0.6	1.2	1.9			21.1		233	15' 8"
5.1	10.2	1.9	0.6			5.7	23.5	12.7	0.6		+		0.6			2.5				28.0		276	16' 3"
7.7	8.3	0.6			7.1	9.0	21.1	17.3			1.3				0.6		0.6	0.6		20.5		351	16' 4"
6.3	13.8	0.6	0.6		6.9	11.3	23.2	40.7			1.3	0.6			0.6	1.9	3.8			29.5		280	16' 5"
5.2	8.5	0.7			30.1	7.2	16.3	24.2									2.0			33.3		281	16' 6"
3.9	14.2	0.6	0.6		1.3	5.8	23.3	58.3			0.6	1.3	1.3		0.6	1.3	3.9			69.9		291	16' 7"
9.1	5.8	2.6			0.6	5.8	21.3	44.0			3.2	5.8	1.9	0.6	0.6	0.6	4.5	0.6		5.2	1.9	195	17' 0"
6.3	1.9	3.2			1.3	5.1	26.6	44.3			1.3	7.6	3.8	1.3	1.9	0.6	1.9			6.3		201	17' 1"
4.5	1.9	1.3		0.6	0.6	6.4	25.7	33.4	0.6		4.5	3.2	2.6	2.6			0.6	1.3		4.5	0.6	239	17' 2"
5.8	1.3	2.6	0.6		2.6	10.2	31.3	36.4			1.9	2.6	2.6	0.6	0.6		1.9			6.4		229	17' 6"
7.7	5.1	0.6			0.6	5.8	15.3	17.3		1.3	12.8	1.3			0.6	3.2	35.8	1.3	1.3	8.9		178	18' 0"
11.6	0.6					4.5	10.3	29.7		1.3	6.5	1.3			0.6		23.9	0.6		7.7	0.6	183	18' 1"
6.8	6.2	0.6		1.9	1.9	7.5	31.7	62.2			5.6	4.3					10.6	0.6		8.1		217	18' 2"
7.0	3.2	4.4			1.3	9.5	27.9	65.4			8.9	1.9	1.3		0.6	0.6	5.1			6.4		274	18' 3"

so. He has, however, made his original data available to the author, who has prepared the accompanying pollen diagram published here for the first time. As is readily apparent, Buell was overly cautious of his data. The diagram is in general agreement with the other diagrams from this region, which is of particular significance because it represents the first independent verification of the present author's results on sediments from Carolina bays.

There should be mentioned a discrepancy between Buell's results presented here and those previously published. In describing the gross stratigraphy of Jerome Bay, Buell (1946b) shows a maximum depth of sediments of 11 ft. The samples for pollen analysis, however, were collected somewhat to the east of the deepest point and represent a complete core to the sand at this location (Buell, in litt.). The bay was never revisited for the purpose of obtaining a core from the thickest accumulation of sediments. The precentages listed in the 1945 paper are those shown at a depth of 8.5 ft. in the present diagram.

At 7.5 to 8 ft. below the surface there is a pronounced oak maximum (Zone Ca). The occurrence of peaks of other broadleaf species (birch, hickory, tupelo, and sweetgum) at approximately the same level, and the disappearance of spruce above this level, indicate that this is the same broadleaf maximum present in the other pollen diagrams. The entire core is post-glacial in age. The trends of the pollen curves toward the bottom, however, suggest that the 11-ft. level is probably in the pine-spruce maximum (M3).

Several shifts in percentage composition in the Cb stratum seem to reflect the progressive shortening of hydroperiods and perhaps the progressive drying of the average climate as well. Cypress, which is dominant in an almost continuous hydroperiod, reaches a maximum first. Then tupelo gum, one species of which does best in a regime of intermittent hydroperiods, reaches a maximum at a higher level. Finally Sphagnum, which probably indicates only local and shallow accumulations of water, reaches a maximum next, and declines toward the present surface of the sediments. The same general sequence of maxima is shared by core Si-22 from the filled-in northwest portion of Singletary Lake, with the addi-
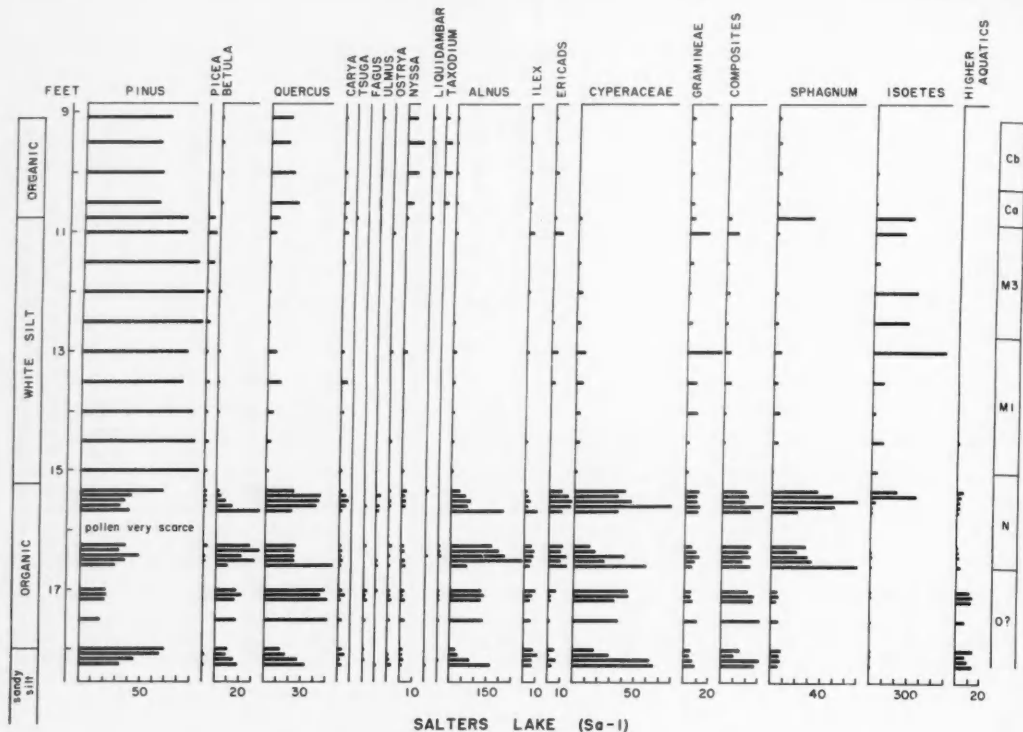
FIG. 6. Pollen diagram of core Sa-1 from Salters Lake.

tion that there are increases in Ilex and composites at the surface, indicating still drier local conditions. Moreover, the same relationship between tupelo and Sphagnum is shown in core B1-1 (Fig. 4).

Buell did not report any hemlock or beech. He found large numbers of fern spores in the lowermost sediments, which undoubtedly were those of Isoetes.

Perhaps it is well to mention one other item concerning Buell's published material on Jerome Bay. In the paper in which he describes the general stratigraphy of the bay (1946b) he discusses the frequency of fire in the Coastal Plain, and states that the black color of the uppermost peat in Jerome Bay has resulted from the charcoal of fires in the bay, and that the similar black color of the surface sediments in the bay lakes has resulted from the importation of charcoal from fires in the nearby regions. However, the common offshore sediment (gyttja) of lakes tends to be black in color, even in regions where fires do not occur, and hence black color *ipso facto* should not suggest the presence of charcoal or the prevalence of fires. The latter certainly are important in the Coastal Plain, and evidence of repeated fires is readily apparent in almost every bay entered. Yet the writer has found definite charcoal fragments very rarely in the cores examined thus far. There is little evidence that fire has destroyed any appreciable por-

tion of the pollen record in the basins considered in this paper.

LITTLE SINGLETARY LAKE (LS-2)

(Figure 10)

Little Singletary Lake lies in a bay located only about 500 yd. to the southeast of Jerome Bay. Both these bays are shown in the aerial photograph in Fig. 4 of Buell's paper (1946b). The sediments in Little Singletary Lake are only 7 ft. thick, but they represent a much longer period of time than do the thicker sediments of Jerome Bay.

The record is quite confused, perhaps through alternate deposition and erosion of littoral organic sediments as a result of expansion and contraction of the lake area. As in the other diagrams spruce first occurs at a particular level, and then is continuously present to the bottom of the core. There is a rather vague pine-spruce maximum (*M*) from 6 ft. to about 8 ft., which is confused by significant percentages of broadleaf trees and of non-tree species as well. The curve for Isoetes, however, agrees moderately well with that of Si-25, in that this spore decreases to small percentages near the top of the second organic layer, suggesting the upper part of Zone *N* in the generalized diagram (Fig. 11). Below a depth of 8 ft. the pollen diagram is even more confused, with a number of sharp changes indicating
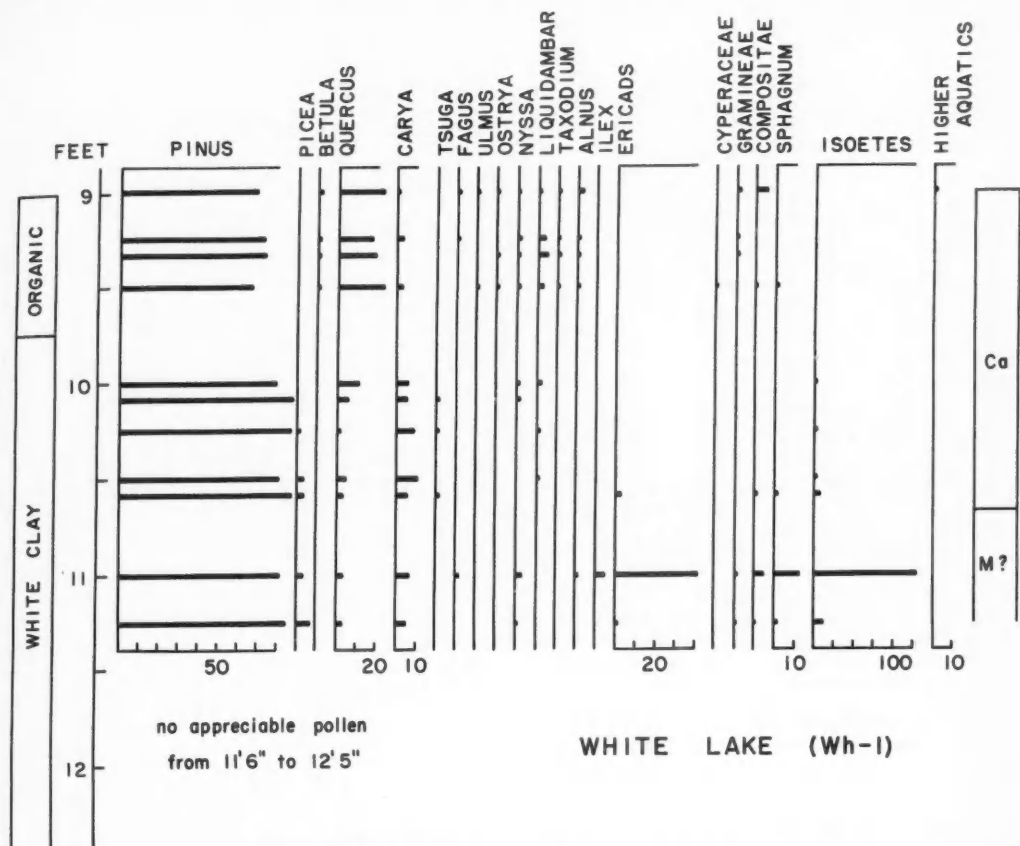
FIG. 7. Pollen diagram of core Wh-1 from White Lake.

discontinuities in the pollen record. On the basis of general resemblances between this pollen diagram and the generalized pollen diagram, however, it seems that zones *N*, *O*, and *P* are represented. Moreover, the marked increase in pine at the bottom with an associated large representation of Isoetes suggests that this stratum may actually date from an earlier time than that represented by the lowermost stratum in Si-25. This zone, which has been designated *Q*, is believed to date from the earliest advance of the glacier in Wisconsin time (Iowan), the reasons for which are given in the discussion of the generalized pollen diagram. Associated with the increase of Isoetes in Zone *Q* are a peak of Alnus and lesser peaks of grasses, composites, and Sphagnum.

SIZE-FREQUENCIES OF ISOETES MICROSPORES

In the sediments of Little Singletary Lake and of Salters Lake there are two distinct sizes of Isoetes microspores, with almost no overlapping in their size-frequency distributions. At a depth of 8 ft. in core LS-2 the smaller spore had a mean size of 26.0 ± 0.24μ (105 spores), which as reported in a previ-

ous paper (Frey 1951) is almost exactly the size of fresh microspores of *Isoetes englemanni* from North Carolina, 26.2 ± 0.15μ (100 spores). The larger spore at this depth had a mean size considerably and significantly greater, 38.2 ± 0.97μ (100 spores). In a random count of 150 microspores from this level, 70% were of the smaller species.

PERCENT UNKNOWNS

It is highly desirable in palynological studies to gradually accumulate in the literature complete analyses in tabular form of the most significant cores that are investigated, so that workers other than the particular authors will have the opportunity to rework the data and rethink the problem, possibly coming up with new interpretations. For this reason the complete data for the cores from Jones Lake, Bay B1-1, and Salters Lake are presented in tables 1, 2, & 3, respectively.

Several aspects of these tables and of the one for core Si-25 previously published deserve to be pointed out. The percentages of grains classified as "unidentified" or "unknown" vary from only a few percent up to several hundred percent. Grains in this
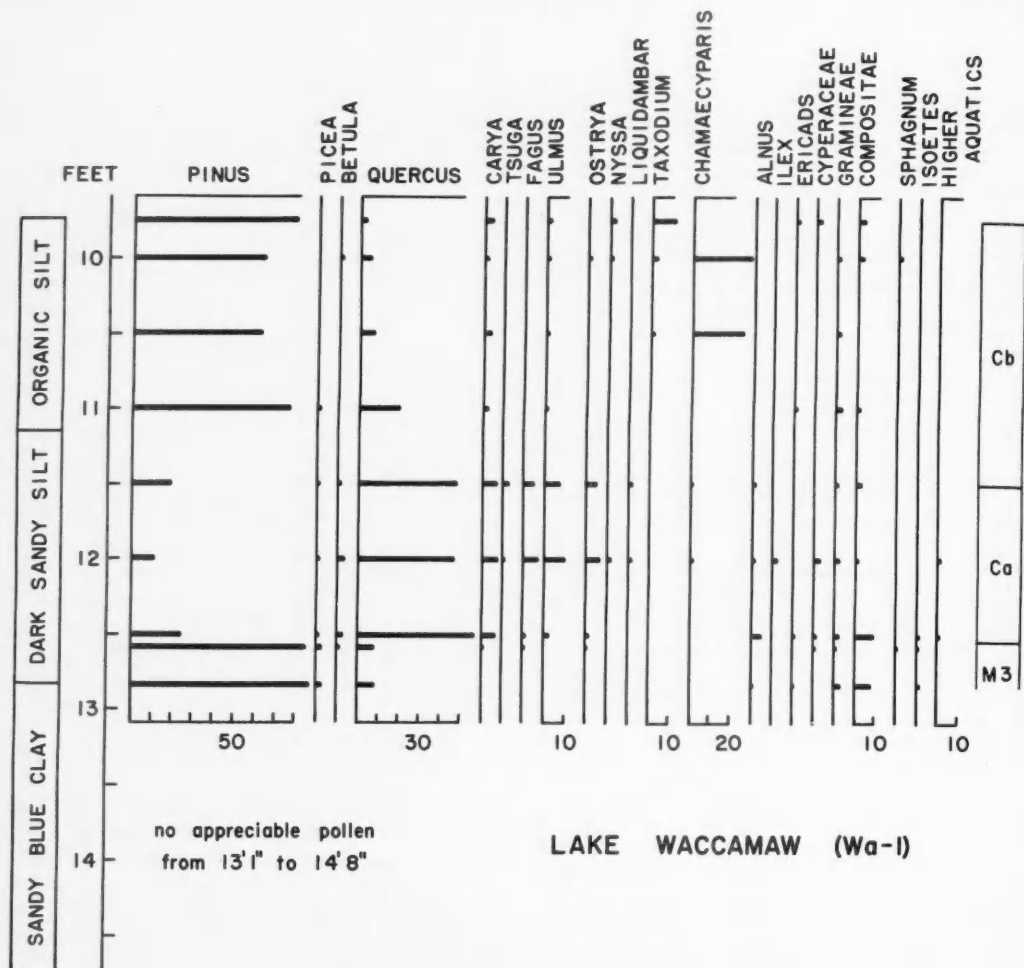
FIG. 8. Pollen diagram of core Wa-1 from Lake Waccamaw.

category are primarily of non-tree types, although in those horizons where the surface details of the grains tended to be obscured by internal clay and silt particles, small percentages of trees may be included. By and large, though, the percentages of unidentified grains seem to reflect the relative abundance in the region of shrubs and herbs other than the types specifically recognized and tabulated. Curves showing the variation in unknowns with respect to depth follow quite closely the curves for tabulated shrubs and herbs (excluding pteridophytes and bryophytes), except in zones *O* and *P* where the relationship is much less close.

If all four tables are considered together the fluctuations in the percentages of unknowns appear to follow a definite pattern. The percentages are almost invariably lowest in *M3* at the time of the Mankato pine-spruce maximum, indicating a very small representation of herbs and shrubs among the vegetation of this period. There follows a distinct increase in unknowns in the post-glacial broadleaf maximum, which is correlated with the peaks of herbs and shrubs in Zone *Ca* in the generalized pollen diagram. This in turn is followed by a decline in more recent sediments. The highest percentages of all, however, occur in zones *N* and *O*, and these, too, are correlated with pronounced percentages of recognized non-arboreal types. However, as already stated, the correspondence between the two series of percentages in *O* and *P* is not so close as in the other zones, possibly indicating the presence of completely different types of non-arboreal plants during these intervals. The identification and tabulation of as many of these unknowns as possible will undoubtedly yield much important information concerning the climatic and edaphic conditions present at these particular times.
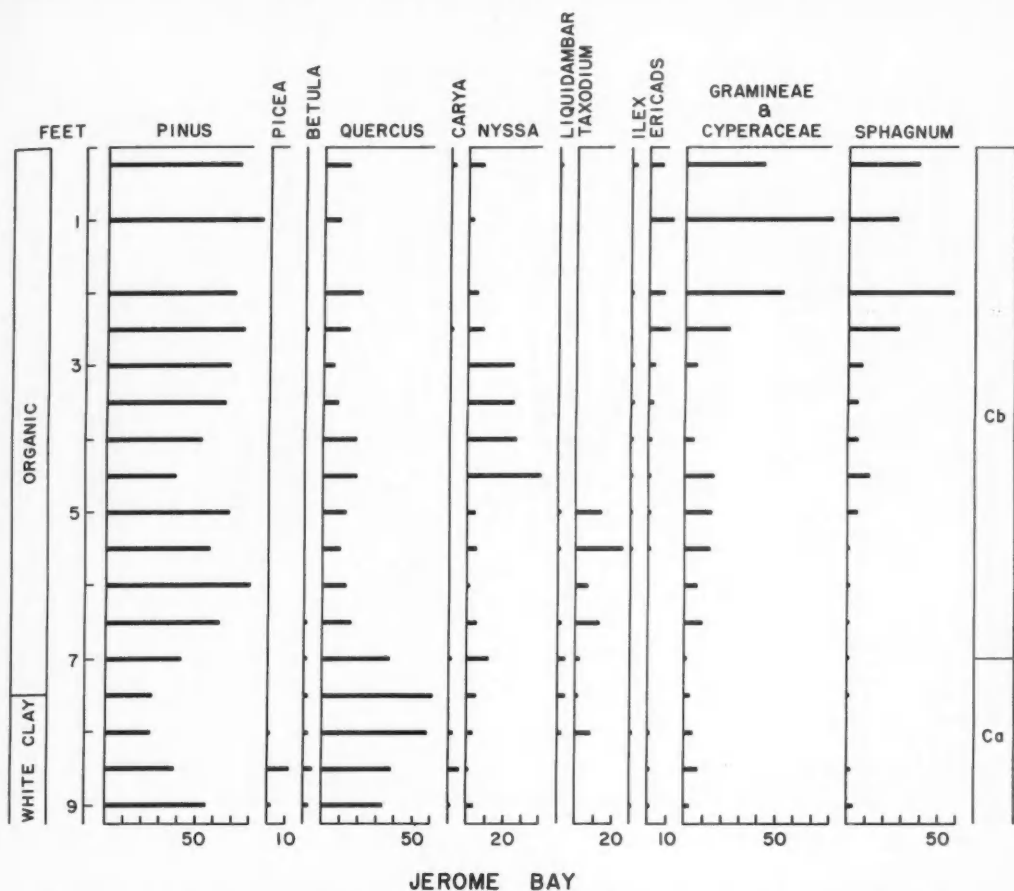
FIG. 9. Pollen diagram of core from Jerome Bay, based on hitherto unpublished data of M. F. Buell.
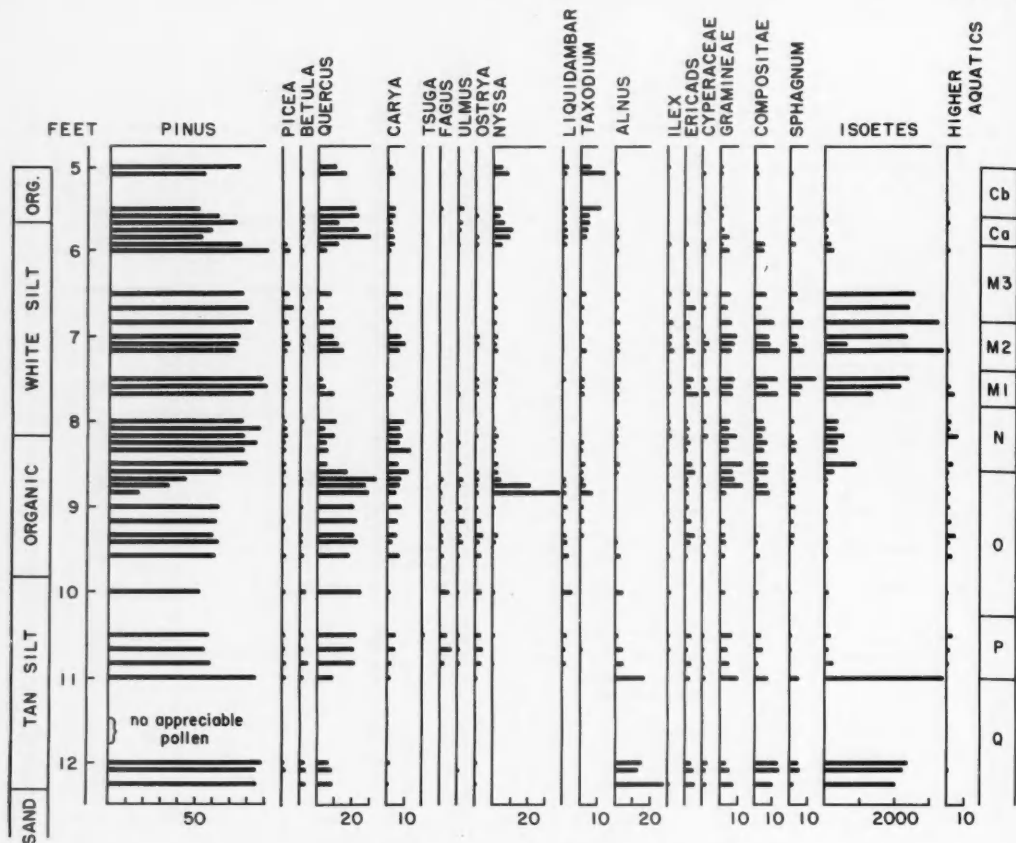
PINE RATIOS

An attempt was made to discover some index to the degree to which the sediments had been worked over by currents and/or organisms. Sponge spicules are present at most horizons in the sediments, and an index based upon the number of intact spicules as compared with fragmented spicules is a distinct possibility. However, spicules were not tabulated during the regular counts, and it did not appear feasible for the purpose of this paper to reexamine the slides for sponge spicule ratios. Rather it was thought that data already at hand on the proportion of whole pine grains to fragmented pine grains might yield a ratio with similar significance. Pine grains have the advantage over sponge spicules for this purpose in that they are present in considerable abundance in all the samples. The pine index used is the ratio of intact grains to grains represented by two separated fragments (undoubtedly from different grains), each consisting of a bladder plus a portion of the body of the grain.

In general the pine ratios are highest (averaging

about 4, meaning that the intact grains are 4 times more numerous than fragmented grains) in the post-glacial sediments, particularly those from Zone Cb. This is to be expected, because the sediments appear to have been laid down with a minimum of subsequent disturbance. The ratios are distinctly lower in the M zone (averaging about 2) which also is to be expected because of the large proportion of inorganic material present, and the molar action that can result through movement of this material. What was not expected is that the pine indices tend to be lowest in Zone N, averaging about 1.5. This horizon is distinctly organic, exhibiting a recurrence of mesophytic broadleafs along with exceptionally large percentages of shrubs and herbs. The low pine ratios may indicate a great activity of benthos in working over the accumulating organic matter. An abundance of diatom frustules in this layer also seems to point to a distinctly higher trophic level.

One definite observation that does emerge from this study is that the pine ratios in Little Singletary Lake are uniformly small throughout the core, the

LITTLE SINGLETARY LAKE (LS-2)

FIG. 10. Pollen diagram of core LS-2 from Little Singletary Lake.

maximum ratio exhibited by any spectrum being only 1.9, with many of the ratios being less than 1. This low frequency of intact pine grains substantiates the conjecture previously made that the stratigraphy of Little Singletary Lake has been confused and complicated by frequent erosion and redeposition of its sediments.

GENERALIZED POLLEN DIAGRAM

With so few pollen diagrams available as yet from the Coastal Plain of North Carolina it is perhaps premature to present a generalized pollen diagram for the region. Nevertheless, one is presented (Fig. 11) with a realization that many of the finer details of the pollen stratigraphy are not yet clearly understood. The gross changes, however, are consistent enough, so that Fig. 11 can be regarded as a first approximation to the actual pollen succession of the region. The generalized pollen diagram has been divided into zones to facilitate discussion, and the extent of each of these zones is shown on the indi-

vidual pollen diagrams. The European practice is to designate the major zones by Roman numerals, with I at the bottom. Inasmuch as there is always the possibility that still older strata might be discovered, the writer has adopted the more flexible system of letter designation. The sequence of the letters M, N, O, and P implies that a continuous sedimentary record is represented, although this is not absolutely certain. In a record as long as this one, represented by such a thin overall depth of sediments, certain portions of the record, as already explained, might very well not be represented, either through non-accumulation of sediments during an unfavorable period or subsequent erosion of sediments and obliteration of the previously existing record. It is believed, however, that the composite record is reasonably complete for the time interval represented.

No single diagram shows to advantage the complete pollen succession as represented in the generalized diagram, although core Si-25 comes the closest.
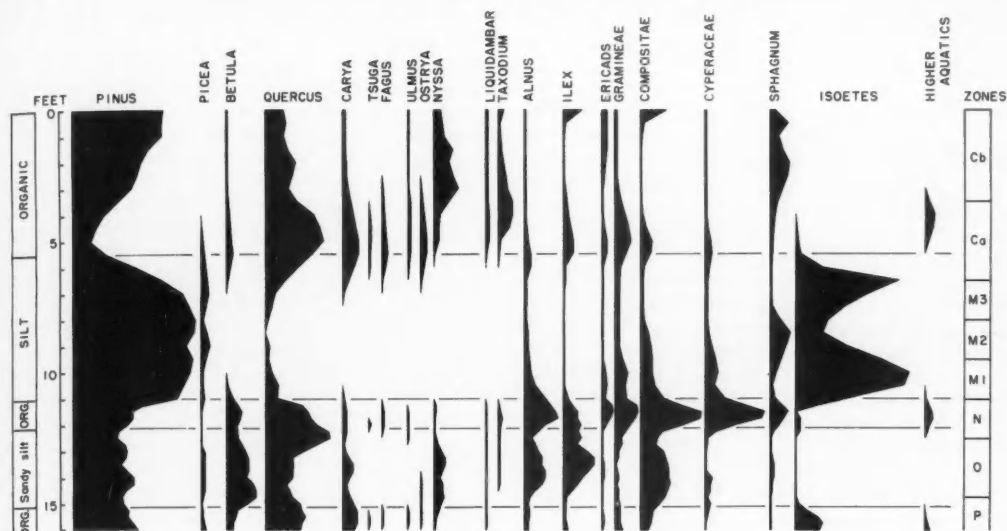
GENERALIZED POLLEN DIAGRAM FOR BLADEN COUNTY, N.C.

FIG. 11. Generalized pollen and spore diagram for Bladen County, North Carolina.

In the generalized diagram the pollen succession of Zone C is based on cores Si-12, Si-22, Si-25, B1-1, and Jerome Bay. Zone M is based on cores J-1, Sa-1, and Si-25. The pollen curves in these two zones are presumed to represent the general sequence in the region, although in constructing the curves it was difficult to decide the relative importance of details from one diagram to another. The pollen curves in Cb are for a filled-in bay, rather than a still extant lake, and probably mirror edaphic changes rather than climatic, as will be discussed presently. The nature of these differences will be obvious in the comparison of the curves for B1-1 (Fig. 4) with Si-25 (Fig. 2).

The pollen curves for the N, O, and P zones are based primarily on the data from core Si-25. These data have been smoothed once by a moving average of three to help emphasize the major fluctuations in percentage composition, and to help minimize those fluctuations which may have resulted from sampling error. Tsuga and Fagus were not found in Zone N in Si-25; but since these two trees do occur in the other cores in which this zone is represented (J-1, Sa-1, LS-2), small percentages of these trees have been inserted in the generalized diagram without at the same time adjusting the percentages of the other trees to keep the actual total at 100%. Similarly, to better represent average conditions as shown in the other diagrams, the grass maximum in Zone N has been made somewhat bigger than it actually is in core Si-25.

As a final word about the construction of the generalized diagram, the vertical scale is only an approximation as to what one might expect to find in

a filled-in bay of moderate size. A linear time scale on the vertical axis is not implied.

In the discussion of the generalized diagram to follow it is well to keep the facts or data of this study separate from the basic assumptions and hypotheses. The facts are based on the gross lithology of the sediments, the microfossil stratigraphy, and the radiocarbon dates.

I. Considering the lithology first, 3 organic horizons tend to occur in these sediments, separated by predominantly inorganic layers, usually silty in nature. The sediments are mainly limnic in origin, except for the most recent sediments of bays or parts of bays without a present persisting free water surface. The only suggestion of an unconformity is at the plane of contact between the uppermost organic layer and the underlying silt layer; in some cores this contact is very sharp. Elsewhere the boundaries between successive lithologic horizons are more or less diffuse in character, with the position of the boundary as shown in the individual pollen diagrams being quite subjectively located.

II. The chief data of this paper are the pollen curves of the individual pollen diagrams. The accuracy of these data are limited first of all by the extent to which the final slide preparations faithfully represent the microfossil populations in the undisturbed sediments, and second by the author's ability to correctly recognize the various pollens and spores as tabulated. Neither the potassium hydroxide method nor the bromoform-acetone method of slide preparation appears to differentially alter the percentage composition of the population. This matter was investigated quite closely in the pollen diagrams. At levels where the pollen curves were changing rapidly,

the use of one method of preparation or the other did not noticeably affect the rates of change. In general, samples from the upper organic layer, or sometimes only from the upper portion of this layer, were prepared by the KOH technique, whereas all other samples, including those from the two lower organic layers (except Zone N in core Si-22) which tended to have a considerable proportion of silt, were prepared by bromoform-acetone differential flotation.

As for correct identification of the various pollens and spores, the author has never had any independent verification of his ability in this respect except the general concordance of the results from Jerome Bay as worked out by Buell. However, all the tree genera, as well as most of the shrub and herbaceous types, are represented in a collection of reference slides, and comparisons were frequently made with the fossil material, particularly in the early uncertain phases of this study. Incorrect recognition of trees and the common non-arboreal types is believed to be one of the lesser errors in this study.

III. On the basis of the radiocarbon chronology now quite securely established for late Wisconsin and post-Wisconsin time, the mesophytic broadleaf maximum in the upper organic layer is definitely early post-Mankato, and the two lower organic layers are definitely pre-Mankato, and quite likely pre-Cary in age.

The basic assumptions and some of the derived hypotheses are the following:

(1) Considering the over-all pollen succession for the region, there do not appear to be any pronounced discontinuities in the record, at least none of the magnitude of thousands of years. The record is believed, therefore, to be essentially continuous.

(2) On the basis of the regular and progressive change in pollen frequencies between the mesophytic maximum of post-Wisconsin time and the underlying pine-spruce maximum, at least in those cores in which this transition is best developed, the upper portion of the pine-spruce maximum is considered to date from Mankato time.

(3) On the basis of the continuous occurrence of spruce from Mankato time to the bottom of the core, and on the basis of the assumption that the over-all sedimentary record is virtually continuous, the lowermost sediments are not believed to break through Wisconsin time into the Sangamon, nor is either of the two lower organic layers believed to be older than Wisconsin time.

(4) Each of these two organic layers (N and P) exhibits a recurrence of mesophytic trees, and since this composition in the uppermost organic layer dates from the mild and favorable climate of an interglacial period, the two somewhat similar populations at greater depths are likewise believed to date from times of glacier withdrawal, in this case interglacial subages in Wisconsin time.

(5) On the basis of other radiocarbon dates the middle organic layer appears to be too old for Cary-Mankato, and is likely therefore Tazewell-Cary. The

next oldest interglacial subage is the Peorian, to which the bottom organic layer has been assigned.

(6) Within the seemingly broad and continuous pine-spruce maximum there is a series of rather minor yet consistent changes in the several pollen diagrams. These changes are believed to be contemporaneous with the Cary-Mankato interval.

(7) Hence, on the basis of certain assumptions and what seem to be obvious correlations, the various zones established in the generalized diagram are assigned to the several glacial and interglacial subages of Wisconsin time. These are described in greater detail in the paragraphs which follow.

In its gross features the generalized diagram is quite obviously divided into a middle zone (M) characterized by a predominance of pine and spruce with an associated abundance of Isoetes, separated both above (Zone C) and below (Zones N, O, & P) by marked increases in oak and associated broadleaf types.

The upper of these zones (C) represents the postglacial period. The basis for this statement is the radiocarbon age of the Ca zone from core Si-25, and the inference that the upper portion of the pine-spruce maximum in M is contemporaneous with the Mankato maximum of glaciation, as already explained. The letter designation C has been given to this zone, because it is considered equivalent to the broadleaf C zones of the glaciated northeast part of the continent (Deevey 1949).

The lower part of the C zone (designated Ca) contains maxima of oak, hickory, hemlock, beech, birch, elm, and hophornbeam. Although not unequivocally so, it appears that the maxima of hemlock, beech, and hophornbeam are reached earlier than oak, which in turn has an associated small peak of grasses. Consequently, the lower part of Zone Ca seems to agree fairly well with Zone $C1$ of the northeastern glaciated region, and the oak-grass horizon with the drier portion of Zone $C2$. Both spruce and Isoetes tend to disappear completely in Ca.

Above the mesophytic broadleaf maximum the record is confused by changes interpreted as the result of edaphic conditions, although there is certainly an over-all decline of broadleaf types in favor of pines, leading to the present pine subclimax of the region. Hemlock, beech, and hophornbeam disappear completely or nearly so from the diagram in this upper zone. The stratigraphic succession of peaks of cypress, tupelo, Sphagnum, and composites-Ilex in that order in the diagrams from filled-in bays and the filled-in portions of lakes are interpreted as reflecting a progressive reduction in duration of hydroperiods and in the amount of standing water available, as already explained. These changes are the kind one would expect to accompany filling of the bays and development of drainage connections with the outside. Changes of this type can be expected to vary considerably from one bay to another, and from one pollen diagram to another within the same bay. (Compare, for example, the diagrams for Si-25 from the open water of Single-

tary Lake with Si-22 from the filled-in portion of the lake at the northwest end).

The only other detailed analyses of the pollen in sediments from the southern Atlantic Coastal Plain are those of Lewis & Cocke (1929) and Cocke, Lewis & Patrick (1934) for the Dismal Swamp in southern Virginia. The sediments sampled are entirely post-glacial (Zone C) in nature, and show a shift from an open grass-sedge meadow at the bottom to a Taxodium-Nyssa-Pinus forest at the top. Detailed comparison with material from Carolina bays will have to await analysis of cores from northern North Carolina, some of which definitely extend back at least to the N interval on the basis of the occurrence of a second organic layer below a layer of silt. There are undoubtedly better sections of Dismal Swamp peat available for analysis than those reported on in the two papers listed above. A diagram in the 1934 paper shows that locally the peat occurs to a depth of at least 15 ft., whereas a 10-ft. depth was the maximum analyzed. Moreover, beneath the peat there may be marine or swamp clay, which, on the basis of the North Carolina pollen diagrams, might very well yield Mankato spectra.

The M zone is the pine-spruce maximum dating from late-glacial time. Somewhat arbitrarily the upper and lower limits of this zone might be established where pine falls below 70% of the total tree pollens present. At its greatest development pine and spruce are essentially the only types of trees represented; even the oak curve tends to pinch out completely. Grains of other broadleaf trees occur erratically, but not consistently enough to be represented in the diagram. It must be assumed either that they were blown in from a considerable distance or that they were derived from the reworking of earlier sediments containing these grains. The rather large representation of these types in the diagram for Little Singletary Lake (Fig. 10) is believed to be the result of the reworking of the sediments by currents, as already explained.

In European diagrams there are three late-glacial zones, of which the middle one—the *Alleröd*—indicates a warming phase in the tundra conditions prevailing. Five radiocarbon analyses yield a mean age of about 10,800 years for this layer, which places it contemporaneous with the Two Creeks (Cary-Mankato) interval in Wisconsin (Flint & Deevey, 1951). The inference is that the zone above the *Alleröd* is contemporaneous with Mankato time, and the zone below with Cary time.

Deevey (1951) has recently reported the finding of a late-glacial zone in northern Maine, which can be divided into 3 subzones designated L1, L2, and L3, with Zone L2 considered equivalent to the *Alleröd* of Europe, and hence dating from Two Creeks time.

Significantly, the present diagrams likewise appear to have the same three zones present, although it is not clear that the middle zone corresponds to a warming in climate as do L2 and the *Alleröd*. In a previous paper (Frey 1951) the author was inclined

to believe that the N organic layer dated from the Cary-Mankato interval, but the minimum radiocarbon age of greater than 20,000 years appears to be too old in comparison with other materials of known Cary-Mankato or Cary age (Flint & Deevey 1951). In view of the vegetational changes in M2 in the North Carolina diagrams, and in the light of present evidence that the Two Creeks interval was of rather short duration, the author is now inclined to regard M2 as dating from Two Creeks time, with M3 representing Mankato time and M1 Cary time. Until the age of the L zones in northern Maine is more definitely assigned to a glacial subage as recent as the Mankato, the author considers it desirable to use a different symbol to designate the apparently corresponding zones of North Carolina.

The M2 zone is characterized by a decline in pine, which is more or less associated with a drastic decline in Isoetes. At the same time spruce tends to increase, and oak virtually vanishes from the diagram. Concurrent increases in composites and Sphagnum are apparent. A short distance below the notch in the pine pollen curve there is an increase in mean size of the pine pollen grains, clearly shown in Figure 4 of the previous paper (Frey 1951). Because all these changes tend to recur in corresponding horizons in the various diagrams (size-frequency distribution of pine grains has not yet been verified for the other sites), the M2 is believed to be real and to have regional significance.

Zone M3 includes not only the pine-spruce maximum of Mankato time but also the incipient transition to the overlying post-glacial mesophytic broadleaf maximum. Oak begins to increase markedly, and occasional grains of hemlock, beech, hophornbeam, etc., begin to appear. A rather constant associated phenomenon is a large peak of Isoetes microspores.

Zone M1 is characterized by substantial percentages of oak, grasses, composites, sedges, and Alnus. These are not entirely the lingering effects of the large maxima in the previous N zone, because at least in the case of oak, grasses, composites, and sedges there are distinct minor maxima in M1.

In the extensive broadleaf zone below the pine-spruce-Isoetes stratum (Zone M) there are at least 3 other zones, represented by two thin organic layers with a predominantly inorganic layer in between. These layers, which can be recognized by such macroscopic features as color and texture, have particular features of the pollen curves associated with them quite regularly, and are here designated as zones N, O, and P.

Zone N is an organic layer characterized wherever it occurs by a great abundance of non-tree plants— Alnus, Ilex, ericads, grasses, composites, sedges, Sphagnum, and higher aquatics. The usual practice in pollen studies is to suspect quantities of non-arboreal pollen in excess of 100% (as is frequently the case in this zone) as indicating treeless conditions. Because the present diagram shows a marked increase in the representation of broadleaf trees as compared

with the pine-spruce zone (*M*), probably indicating, therefore, a considerably milder or at least moister climate, the author is not inclined to believe that the Coastal Plain as a whole was essentially treeless at this time. A more likely explanation is that the Carolina bays were treeless, and that the non-arboreal vegetation in these basins and around their edges produced quantities of pollen which overshadowed that contributed by the trees outside the bays. Such local control of pollen composition in sediments is known to occur, especially on bog surfaces (Faegri & Iversen 1950).

Zone *N* is also characterized by small but consistent percentages of such mesic types as beech, hemlock, elm, tupelo, and cypress. In addition there are fairly marked peaks of birch and higher aquatics. Oak increases toward the bottom of the zone, and pine reciprocally decreases.

Zone *O* is characterized by lesser quantities of oak in the middle than at either end. Associated with the oak minimum are peaks of birch, alder, Ilex, and composites, and a lesser peak of sedges. Beech, hemlock, and elm, which were present in the overlying *N* zone, tend to be absent. Minor peaks of hickory and tupelo bracket the oak minimum above and below.

Finally, in the lowermost *P* zone there is an oak-hickory peak, with an associated recurrence of such mesic types as beech, hemlock, elm, and hophornbeam. Non-tree types are declining, except for Isoetes and aquatic pollens. Near the bottom of *P*, as shown in the generalized diagram, pine and spruce seem to be increasing at the expense of broadleaf types. This shift is well developed at the bottom of the LS-2 diagram, where pine again constitutes more than 80 percent of all tree pollens, and broadleaf trees are represented by only scattered grains of oak, birch, and hickory. If the interpretation of this complex diagram is correct, LS-2 extends somewhat farther back in time than does Si-25.

Both the *N* and *P* zones indicate a more favorable climate through the occurrence of various mesophytic trees, and through the greater accumulation of organic matter. These zones, as previously indicated, have been assigned respectively to the Tazewell-Cary and the Peorian (Iowan-Tazewell) intervals. If the surmise stated in the previous paragraph is true that core LS-2 may be the oldest on the basis of the increase in pine and decrease in broadleaf trees toward the bottom, then logically the pine-Isoetes zone at the bottom could be assigned to the beginning of Wisconsin time—the Iowan glacial subage. This has been tentatively designated as Zone *Q* in the pollen diagram for LS-2 and in Table 4.

In terms of general correlation with perhaps edaphic as well as climatic significance it should be noted that small but consistent peaks of aquatic plants are always associated with the occurrence of hemlock, beech, elm, and hophornbeam. Together these features seem to indicate the occurrence of "wet" periods.

The zonation of the generalized pollen diagram and the criteria or characteristics of each zone are listed in Table 4. In each of the individual diagrams the extent of the various zones represented is shown.

TABLE 4. Subdivision of the North Carolina diagrams by zones, and their presumed ages.

Zone		Pollen and spore characteristics	Deevey (1951) correlates	Radio-carbon age	Supposed age
C	Cb	Increasing pine and decreasing oak; general absence of hemlock, beech, and hophornbeam; edaphic control of hydrophytic trees and shrubs according to duration of hydroperiods.	C3		post glacial
	Ca	Mesophytic broadleaf maximum of oak, hickory, hemlock, beech, elm, and hophornbeam; Picea and Isoetes disappear; minor maxima of non-tree types, and of aquatic plants.	C1-C3	10,224 ± 510	
M	M3	Beginning shift from pine maximum to broadleaf maximum; very few broadleafs at bottom; large Isoetes maximum; upper limit at 70% pine.	L3		Mankato
	M2	Small decline in pine and marked decline in Isoetes; almost no broadleafs; rather pronounced peak of Sphagnum; increase in mean size of pine pollen.	L2		Two Creeks
	M1	Pine maximum, declining at bottom; distinct although minor peaks of oak, grasses, composites, and sedges; lower limit at 70% pine.	L1		Cary
N		Pronounced NAP maxima of Alnus, Ilex, ericads, grasses, composites, sedges, Sphagnum, and aquatics; rise in oak, and recurrence of mesophytic broadleafs; pronounced decline of Isoetes; organic sediments.		>20,000	Tazewell-Cary
O		Oak highest at top and bottom; peaks of birch, Alnus, Ilex, and composites associated with oak minimum; no Isoetes.			Tazewell
P		Oak-hickory maximum, with minor percentages of mesophytic species; NAP declining; aquatic pollen present; Isoetes increasing; increased organic content.		>20,000	Peorian
Q?		Pine and Isoetes abundant, shown only in LS-2; small percentages of oak and hickory but no other broadleafs.			Iowan?

DISCUSSION

In the words of Faegri & Iversen (1950) pollen analysis "has been perfected into a very refined instrument of research, highly versatile and giving surprisingly intimate glimpses into the conditions of life during earlier periods." It is not meant to imply by this quotation that the data presented in this paper are particularly "refined," because as a result of the extremely slow rate of sedimentation in these deposits, the sampling interval employed of 6 in. or even 3 in. was much too great. Nevertheless, the gross fluctuations in the percentage representation of the various types of pollen and spores are probably fairly reliable, because of their general con-

cordance in the several diagrams from the region. The finer details of the succession will have to be worked out later on the basis of fresh cores.

Spruce and fir pollen have been previously reported from a number of localities south of the glacial border in the United States. Many persons have been disinclined to accept the significance of these occurrences because of the possibility of long distance transport. Faegri & Iversen (1950) in reviewing this general subject conclude that the extent of ordinary pollen transport of wind-pollinated species in forested regions is roughly 50 km, but that the forests beyond the 10 km limit are of very little importance in the pollen diagrams; much of the pollen in a particular sample will be derived from much nearer sources. In a forested region the amount of pollen which in European practice is considered possibly of long-distance origin is no more than 5% of the total tree pollens present. The quantity of long-distance pollen relative to locally produced pollen is usually so small that it can be disregarded in forested areas. Similarly, if grains of a particular wind-pollinated species or type are not present in a given spectrum, there is very little chance that this species or type grew in the locality in question at the time represented. In non-forested regions, on the other hand, such as tundra or extensive prairie, all tree pollens in a sample must necessarily have been imported by the wind.

There is no evidence that the Atlantic Coastal Plain at the location under consideration was ever treeless during the time interval represented by the cores studied. The large percentages of non-arboreal types of plants in Zone *N* have already been explained on another basis. Assuming then that a forest cover of some type has been continuously present, the occurrence of a particular type of pollen means that the species of plant which produced this pollen with great probability was growing at least within relatively few miles of the site. Most of the pollen, of course, would be much more immediate in origin. This would be particularly true of insect-pollinated plants, or of wind-pollinated types other than conifers.

The North Carolina pollen diagrams here presented demonstrate pronounced shifts in percentage composition of the pollens and spores of the various tree species and non-tree species. Many of these shifts in composition are obviously of regional rather than local significance. If one is prepared to admit that pollen diagrams do reflect changes in composition of the vegetation producing them, then he must certainly agree that there have been very extensive changes in composition of the vegetation in this portion of the Atlantic Coastal Plain. There was a time, for example, when the trees present were almost exclusively pine and spruce, with only a very small percentage of oak, and possibly no representation of other broadleaf types. Isoetes, generally considered a more northern type, at least in the abundance here encountered, is an almost constant associate. Above

and below this pine-spruce maximum, particularly above, there is a considerable representation of broadleaf types including the mesic beech, as well as some hemlock. In fact, considering the usual overrepresentation of pine pollen and its buoyancy in the air, pine may have been virtually absent from the region during the post-glacial broadleaf maximum.

The question might be raised as to what extent these major fluctuations in the pollen curves have resulted from the differential destruction of pollen grains through natural causes. Grains which are undergoing breakdown can be readily recognized. The exine instead of being intact tends to have holes of irregular shape "eroded" into it. Sometimes the shape of the pollen grain persists, but the amount of material in the exine is so reduced that the grain is only a "ghost."

Horizons containing eroded pollen were very infrequent in these cores. Moreover, it is difficult to conceive how in the pine-spruce maximum virtually all other types of pollen were differentially destroyed leaving the pine grains in untouched condition, whereas in the overlying broadleaf maximum just the reverse susceptibility to destruction occurred. Differential destruction does not account for the observed changes in pollen frequency.

Such major changes in composition of the Coastal Plain vegetation are all the more remarkable because of the opinion held by Berry (1926), Braun (1950), Berry (1952), and others that the vegetation of the higher portions of the Coastal Plain was almost monotonously uniform during the Pleistocene. The Berrys did not list any northern species among the macroscopic remains from the Pleistocene deposits of North Carolina, and Braun, accepting these findings and discounting the occurrence of spruce and fir pollen in isolated instances in North Carolina (Buell 1945, 1946a) and South Carolina (Cain 1944), reaffirms this uniformitarian idea.

Braun conceives of the vegetation of the Atlantic Coastal Plain during the Pleistocene as being essentially similar to what it is today—predominantly pine on the edaphically less favorable sites, deciduous broadleafs on more favorable sites characterized by slope, greater organic content, and better moisture conditions, and Southeastern Evergreen Forest in the bays and pocosins.

Presumably the peripheral portion of the Coastal Plain was alternately expanded and contracted by the lowering or raising of sea level resulting from the major advances and retreats of the ice sheet, although there is some question as to how extensive such fluctuations were within Wisconsin time alone. At any rate, Braun believes that the newly exposed surfaces were first invaded by pines from the higher more stable portions of the Coastal Plain, and that as the recently exposed land subsequently developed richer soils and better drainage, mesophytic species migrated down the rivers from the upper levels of the Coastal Plain and Piedmont to suitable edaphic sites. Because of the supposed lack of climax forest, based upon the present pine subclimax in the Coastal

Plain, Braun considers that northern and southern species of plants were able to migrate with relative ease up and down the ecologically unstable peripheral strips of the Coastal Plain in response to changing climate and pressures in the glacial and periglacial regions. The inference is that such an influx of northern species at the periphery could account for the occurrence of spruce and fir pollen in the Coastal Plain deposits farther inland.

Singletary Lake is located approximately at the position of the Surry scarp, as described by Flint (1940). The present elevation of the lake (63 ft.) places it on the seaward side of the scarp. If Flint's surmise concerning the age of this scarp is correct, this bay, and possibly all the other bays described in the present paper, were covered by the sea during the Yarmouth interglacial age. The sediments in Singletary Lake, constituting one of the longest records to date, do not extend back to Yarmouth time, or even to Sangamon time. The lowest organic layer has a probable age between 30,000 and 100,000 years, based upon observed minimum and presumed maximum rates of sedimentation (Frey 1951), with the lowermost horizon probably being early Wisconsin in age. There is no evidence of a marine invasion during this period: spicules of freshwater sponges occur throughout the sediments, and there are no marine fossils known to date. Hence, this region of the Coastal Plain has been continuously above sea level for at least several tens of thousands of years.

During this long period from somewhere within Wisconsin time to the present, the vegetation of the North Carolina Coastal Plain has not been uniform. It has not consisted of a pine subclimax in its present aspect, with a great variety of broadleaf communities in suitable edaphic situations. Rather it has experienced very drastic changes in composition, which appear to be correlated with the major changes in position of the ice front in Wisconsin time or, better stated, with the contemporaneous regional changes in climate (temperature and/or available moisture) during this period.

If one feels inclined to explain the presence of spruce, fir, and perhaps hemlock pollen on the basis of long distance transport, then why should he not also expect a recognizable representation of the various broadleaf genera during the pine-spruce period from the supposedly persisting deciduous forests of the Piedmont and mountains? Odum (1952), for example, has constructed a hypothetical Pleistocene weather map which shows strong winds from the northwest, roughly paralleling the present orientation of the Carolina bays. These winds would be expected to transport other pollens than just pine, spruce, and fir.

Furthermore, the pollen of *Magnolia virginiana*(?) and Gordonia are readily recognizable. Yet these two trees, which at present are characteristic of the broadleaf evergreen community of many of the Carolina bays, are not represented in the pollen diagrams until well after the post-glacial maximum (Fig. 5).

The inference is that they, and probably other components of the Southeastern Evergreen Forest as well, have not reinvaded the North Carolina Coastal Plain until quite recently. This may possibly be the edaphic consequence of most of the Carolina bays persisting as lakes up until fairly recent time (upper *Ca* time), although there should have been plenty of lowland locations in river floodplains where these species could have persisted during this period, other conditions being favorable. Moreover, the present bay lakes tend to have Magnolia and Gordonia in their peripheral fringe of broadleaf evergreens, so that present day conditions are suitable for these trees even when most of the area of the bay is in standing water. It is quite certain, therefore, that there have been types of trees and other plants present in the past which now no longer occur in the region, and conversely there are now present in the region certain types of trees which were not continuously there during Wisconsin time. The eventual detailed study of the non-arboreal pollens and unknowns will undoubtedly provide many more examples.

One of the big problems in phytogeography at present is the extent to which the vegetation south of the glacial border was affected by changes in climate coincident with advances and retreats of the ice sheet and was modified by invasions of plants from the north. Braun (1950) states that the Atlantic Coastal Plain and the floodplains of the Mississippi Embayment probably experienced considerable influx of northern species because of their recent formation and lack of forest climax, but her main thesis is that the great deciduous forests in the other physiographic provinces of the Southeast remained essentially unchanged beyond a distance of perhaps 50 mi. from the glacial border. The evidence for this idea is primarily the present distribution of plants in this region, with which Braun is intimately acquainted. Moreover, it has been shown quite recently that the effects of frost action on physiography and soil structure are perceptible for only a few tens of miles south of the glacial border in eastern North America, and that there was no permafrost in the periglacial region (Raup 1951; Denny 1951).

Deevey (1949), on the other hand, conceives of the climatic changes south of the glacial border as having been so extensive that all the mesophytes, including the "Miocene relics," occurring there in pre-Pleistocene time were forced southward, perhaps into Florida and Mexico. Evidence marshalled in support of this opinion is based largely on animal distribution, and on the occurrence of animal and plant macro- and microfossils. The recently published paper by Huntington (1952) on the purple grackle lends considerable support to this viewpoint.

In spite of evidence (summarized by Braun 1950, 1951) of truncated distributions of plants, persistence in microhabitats (grottos) in the periglacial region, etc., the author feels that the North Carolina pollen diagrams indicate a fluctuation in climate even during Wisconsin time of considerable magnitude,

and, by inference, probably an even greater fluctuation during the Pleistocene as a whole. It is unfortunate that all the Carolina bays, with their invaluable records of past vegetations and climates, are confined to the Atlantic Coastal Plain. Pollen diagrams from the inland forest regions south of the glacial border are bound to continue to be few in number because of the general paucity of basins of sedimentation in this region. The analysis of cores from bays farther south in the Coastal Plain should throw additional light on the magnitude of the latitudinal shifts in vegetation in this province during the Pleistocene, and, by inference, the magnitude of the climatic shifts that probably occurred farther inland.

The author apologizes that much of the discussion in this paper has centered around the stratigraphic occurrence of the various plant microfossils and the correlation of these from one diagram to another, rather than around the vegetation that must have been present to produce these microfossils, and the various climatic regimes and/or edaphic and physiographic conditions indicated. The latter will probably take some time to unravel satisfactorily, and certainly will require the efforts of many investigators. A number of tentative deductions can be pointed out, however.

The pine-spruce maximum in zones $M2$ and $M3$ exhibits only erratic occurrences of broadleaf trees and of shrubs and herbs. Moreover, the percentages of unknowns are low, especially in $M3$. This indicates that pines were by far the predominant trees at this time, possibly with a few spruces around the edges of some of the bays. Apparently very little ground cover was present, which would make it possible for particles of silt and clay to be blown from the exposed surfaces into the bays, thereby helping to account for the silty sediments of this interval. Such inorganic substrate would be favorable to the growth of Isoetes, and the high percentages of this usually semi-aquatic plant might indicate that the littoral portions of the lake basins were largely exposed at this time. The general interpretation might be that M time was quite dry. This interpretation, however, is difficult to reconcile with the virtual absence of oaks, a number of which are definitely xeric species occurring in the region today and should be represented. It is also somewhat difficult to reconcile the xeric hypothesis with the occurrence of peridinians (identified by R. H. Thompson), which are most abundant in the inorganic sediments, especially those of the M zones. These microfossils occur in all the bays at particular contemporaneous levels.

Mesophytic trees and vascular aquatic plants tend to occur together in the three organic layers. The presence of higher aquatics does not necessarily mean that the bays were filled with water only at these times, because the acid Bladen County bay lakes have almost no higher aquatic vegetation in them today, and certainly none of the three commonest genera from the mesophytic zones—Myriophyllum,

Nymphaea, and Nuphar. On the other hand, Lake Waccamaw although very similar to the Bladen County lakes in many respects has conditions sufficiently more favorable (including a higher calcium content) to permit the occurrence in abundance of quite a number of species of submersed and floating-leaf aquatics. The zonal occurrence of aquatic plant pollen in the cores, therefore, may well indicate more generally favorable chemical conditions in the water at these times. The only corroboration of this interpretation at hand is a preliminary chemical analysis of core Si-1 made by H. T. Odum in 1948. Calcium is relatively low (approx. 0.01% of the dry weight of the sediments) from the surface down through Zone M, and then more than doubles in Zone N, where the aquatics and mesophytes occur. Chemical studies of the sediments are one of the as yet virtually unexploited methods of attacking the stratigraphy of these basins.

The post-glacial mesophytic maximum presents its peculiar problems. Is it conceivable that mesophytes could occupy the Coastal Plain including the relatively xeric sand ridges to the virtual exclusion of pines? Yet that is what seems to have happened judging from the pollen record. At any rate, the present pine subclimax, which is currently stated to be maintained by high frequency of fires, was not established in early post-glacial time, and the over-all aspect of the vegetation then must have been very different from what it is now.

These previous remarks point to some of the difficulties in interpreting the causes of these vegetational changes, and serve to emphasize that probably no single factor such as moisture or temperature can be the complete explanation. If the author's interpretation is correct that the vegetational fluctuations as recorded in the pollen diagrams are correlated with the advances and retreats of the Wisconsin ice sheet, then vegetational controls in the Southeast were very likely a complex of temperature, moisture, and edaphic factors.

SUMMARY

The microfossil records in 8 cores from the southeastern portion of the North Carolina Coastal Plain are enough similar so that generalizations can be drawn concerning the regional fluctuations in microfossil representation, and consequently in the fluctuations for this region of the vegetations which must have produced these microfossil populations. The evidence shows clearly that since early Wisconsin time this region has experienced quite a number of major shifts in vegetation, which, partly on the basis of radio-carbon dates, appear to be correlated with the several glacial and interglacial subages of Wisconsin time.

The most recent mesophytic broadleaf maximum is definitely post-glacial (or interglacial), with a radiocarbon age of approximately 10,000 years. At a slightly greater depth, with a continuous and progressive change in pollen composition in between,

there is a pine-spruce maximum, which by inference dates from the Mankato period in Wisconsin time. On the basis of these two conclusions and the further fact that the age of both a second and a third organic layer occurring at greater depths exceeds 20,000 years, a tentative time table has been established, in which the occurrence of broadleaf mesophytes plus hemlock indicates interglacial subages in Wisconsin time. On the basis of this type of reasoning, the lowermost sediments examined would date from earliest Wisconsin time (Peorian).

The Cary-Mankato substage is not represented by the same degree of vegetational changes as the other supposed interglacial substages. One of the correlates in an increase in mean size of pine pollen, indicating possibly the disappearance of the northern *Pinus banksiana* (if this is the species represented by the small grains) and the possible invasion by some of the species of pine presently occurring in the region, all of which have quite large grains.

If one believes that the forest composition changed little in the southeastern states during the various phases of the Wisconsin glaciation, and that during the glacial subages the mixed mesophytic forest of the Southern Appalachians was perhaps displaced only to somewhat lower elevations, then one might expect that a substantial occurrence of hemlock, elm, hophornbeam, and perhaps beech, at the present locations, would be correlated with a glacial advance, or in other words with a maximum depression of climate. This is contrary to the present findings.

The over-all picture of the changing vegetation of this region is that the present pine subclimax has not been continuously present since shortly after the region emerged from the ocean in mid-Pleistocene time. Ten-thousand years ago pines were of only minor importance in the forest cover of the Coastal Plain at this location; mesophytic broadleafs predominated. During the Mankato period pines were present along with some spruce, almost to the exclusion of the broadleaf types, but size-frequency studies indicate that different species of pine were dominant in the region then than the present *P. palustris-taeda-echinata* composition. Other similar major shifts have occurred at earlier periods in Wisconsin time.

The writer is not inclined to believe that these pronounced shifts were solely the result of edaphic succession in a physiographic cycle which even now is not very far advanced, or of vegetational instability in a region where forest climax had not yet developed. Climatic fluctuations undoubtedly occurred, correlated with advances and retreats of the Wisconsin ice sheet. Purely by inference at this time it is believed that the climate at more inland locations also varied during this period, and that the climax forests of these locations probably experienced considerable displacements.

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